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Web links to the author's journal account have been redacted from the decision letters as indicated to maintain confidentiality.

17th Jan 22

Dear Dr Carraro,

Your manuscript titled "Structure of dendritic river networks shapes ecological dynamics" has now been seen by 2 reviewers, whose comments are appended below. You will see that they find your work of some potential interest. However, they have raised quite substantial concerns that must be addressed. In light of these comments, we cannot accept the manuscript for publication, but would be interested in considering a revised version that fully addresses these serious concerns.

We hope you will find the reviewers' comments useful as you decide how to proceed. Should additional work allow you to address these criticisms and meet our editorial thresholds outlined below, we would be happy to look at a substantially revised manuscript. In the following, we list our editorial thresholds:

- Provide compelling evidence that Optimal Channel Networks (OCNs) more accurately estimate real river metapopulation parameters, namely coefficient of variation for a metapopulation and metapopulation capacity, than other synthetic network analogues, such as random branched networks (RBNs) and balanced binary trees (BBTs);
- Robustly support your claims by evaluating derived values against observational metapopulation data from real river network(s);
- Provide a balanced, in-depth discussion of the origins of differences in performance between synthetic networking approaches and, where relevant, caveat or tone down statements to reflect uncertainties and/or simplified assumptions within your analysis.

If you choose to take up this option, please either highlight all changes in the manuscript text file, or provide a list of the changes to the manuscript with your responses to the reviewers.

Please bear in mind that we will be reluctant to approach the reviewers again in the absence of substantial revisions.

If the revision process takes significantly longer than three months, we will be happy to reconsider your paper at a later date, as long as nothing similar has been accepted for publication at Communications Earth & Environment or published elsewhere in the meantime.

We understand that due to the current global situation, the time required for revision may be longer than usual. We would appreciate it if you could keep us informed about an estimated timescale for resubmission, to facilitate our planning. Of course, if you are unable to estimate, we are happy to accommodate necessary extensions nevertheless.

We are committed to providing a fair and constructive peer-review process. Please do not hesitate to contact us if you wish to discuss the revision in more detail.

Please use the following link to submit your revised manuscript, point-by-point response to the reviewers' comments with a list of your changes to the manuscript text (which should be in a separate document to any cover letter) and any completed checklist:

[link redacted]

** This url links to your confidential home page and associated information about manuscripts you may have submitted or be reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage first **

Please do not hesitate to contact me if you have any questions or would like to discuss the required revisions further. Thank you for the opportunity to review your work.

Best regards,

Dr Clare Davis
Senior Editor
Communications Earth & Environment

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EDITORIAL POLICIES AND FORMAT

If you decide to resubmit your paper, please ensure that your manuscript complies with our editorial policies and complete and upload the checklist below as a Related Manuscript file type with the revised article:

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For your information, you can find some guidance regarding format requirements summarized on the following checklist:(<https://www.nature.com/documents/commsj-phys-style-formatting-checklist-article.pdf>) and formatting guide (<https://www.nature.com/documents/commsj-phys-style-formatting-guide-accept.pdf>).

REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

I enjoyed reading this manuscript. Please see my attached review.

Reviewer #2 (Remarks to the Author):

Thank you for the opportunity to review this manuscript. The authors argue that Optimal Channel Networks (OCN) create realistic representations of river networks and can more accurately capture metapopulation properties than random branching networks (RBN) and balanced binary trees (BBT). Overall, I found these arguments to be well supported and believe this paper makes a valuable

contribution to increasing our theoretical understanding of riverine metapopulations. Before publication however, I have some minor recommendations for the authors:

Figure1: Include an OCN network adjacent to BBT and RBN with similar parameter values in top row. It was difficult to understand how AT values were used to standardize/compare networks since BBT and RBN are not related to area. An additional panel should help readers understand that N can be extracted from an OCN (with an AT) and used to create comparable BBT and RBN (before reading the methods).

Line 73: Typo. “functional” should be “function”

Line 107-113: Consider adding an image of an artificial network labeled with terms in glossary (links, nodes, confluences, etc.). A supplementary figure would complement the existing definitions and eliminate any misunderstanding regarding the derivation of Pr. For example, to understand Pr the reader needs to know that a link is between confluences (or a source and confluence) and not between two nodes (as it is sometimes defined).

Line 124: “scale dependency” is better than “problem of scaling”. I do not think scaling is a problem per se. The problem is more that metrics can change with scale of observation (see figure 1 in Jackson and Farhig 2015. Global Ecology and Biogeography for a conceptual diagram). Scaling only becomes a problem when the change is not predictable.

Line 126-132: I found it confusing that the paragraph above dismisses Pr for being scale dependent while this paragraph recognizes scale dependence is ubiquitous and important. Thus, it seems like Pr can be both undesirable and desirable because of scale dependency? If this was not the intended interpretation, changing the order of the paragraphs may help clarify.

Line 142, 156: Provide more detail regarding power-law scaling as it pertains to Figure 3c. This would fit well with the text explaining 3a and 3b in the supplement. Specifically, describe the salient features of “ $P[A > a]$ as a function of a ” from the citations provided. This should help the reader better understand the scaling results.

Line 168: How were connectivity patterns chosen? Clarify that the different methods used to create artificial stream networks produce different connectivity patterns.

Line 216: “Correct ecological conclusions” may be too strongly worded because this study was mostly theoretical. I think it would be better to state that OCN produce conclusions that are consistent with those obtained from real stream networks (which may or may not be “ecologically correct”).

Line 220: If possible, a discussion, either here or in the introduction (Line 54), outlining the specific stream network attributes OCNs allow us to generalize and how this helps us understand the ecology of real stream networks would be valuable. Since it is becoming rather routine to extract real river networks from either digital elevation models or digital flowlines, why not use real stream networks or the geometry directly measured from them for analysis?

Line 278: Correct citation to (Zimmerman and Ver Hoef, 2017)

Sincerely,
Darin Kopp, PhD

Review of Structure of dendritic river networks shapes ecological dynamics by Carraro and Altermatt

The manuscript by Carraro et al. reviewed methods for river network delineation and pointed to potential problems of a common method - branching probability. The manuscript is very well written and addresses an important topic in stream ecology. I liked the brevity of the manuscript, the beautiful figures, and how they deliver information. However, I am afraid that some of their claims seem to be built upon the misinterpretation of previous research (if I understood their writing correctly). In general, I support the publication of this manuscript, but it would require a substantial reconsideration of the manuscript content. I listed my concerns below:

Major comments

Branching probability. One of the most important findings in this research is that branching probability is not a “scale-invariant” feature of river networks - the authors claimed in L122-123 “branching probability is a non-descriptive property of a river network, which by no means describes its complexity, and depends on the observational scale.” However, I’m afraid I have to disagree with this statement. To explain this, let me use the Strahler ordering scheme (this is similar to A_T in terms of “observation scales”). River networks are often claimed as an outstanding example of fractal, and the Horton’s bifurcation/length laws are used as the basis of such a claim. Specifically, the bifurcation/length ratio (R_B and R_L) follows geometric-scaling relationships such that:

$$\begin{aligned} R_B &= N(\omega - 1)/N(\omega) \\ R_L &= L(\omega - 1)/L(\omega) \end{aligned}$$

where ω is the stream order, and $N(\omega)$ and $L(\omega)$ refer to the number of links and the average length at the order ω , respectively. Here, stream order ω is a resolution-dependent measure because we may find finer 1st order streams as we increase the resolution (smaller A_T value). Nevertheless, the above laws remain valid regardless of the resolution or A_T values, i.e., the limiting channel network is a fractal with properties related to R_B and R_L .

Branching probability has the same property. Let me assume that the link length follows an exponential distribution with a rate parameter λ . Under this assumption, Packham & Gupta 1999 (Water Resources Research) has shown that the segment length of any stream order ω , L_ω (i.e., from one confluence at which stream order ω begins to another confluence at which stream order $\omega + 1$ begins), will follow an exponential distribution (see equations 17-26 in their paper). More importantly, they found that the cumulative probability distributions of segment length at orders ω and k are identical after simple rescaling as:

$$1 - \exp(-\lambda p_\omega x) = 1 - \exp(-\lambda p_k (R_L^{k-\omega} x))$$

where $p_\omega = R_L^{-(\omega-1)}$, λ the rate parameter, and x a given segment length. Note that the above equation shows the equivalence of branching probabilities measured at different scales - the left side is the branching probability at stream order ω ($Pr(L_\omega < x)$) and the right side is that at stream order k ($Pr(L_k < R_L^{k-\omega} x)$). Therefore, branching probability remains constant across stream orders after multiplicative rescaling. Packham and Gupta 1999 showed that this statistical self-similarity was indeed observed in natural river networks. While Packham and Gupta 1999 assumed an exponential distribution for the link length, they also showed that the above result holds true for any statistical distributions in an asymptotic sense.

If I understood correctly, what the authors performed in Fig. 1 is similar to the above exercise - they pruned smaller tributaries from the network by increasing A_T (e.g., removing only 1st order streams) and calculated branching probabilities for the pruned networks. However, their comparison of branching probability is misleading because they did not perform proper rescaling when evaluating statistical similarity across scales. Therefore, in my opinion, their claim is not justified.

When random river networks can/cannot be used? While I agree that RBNs lack some important characteristics of real river networks (e.g., area scaling), I don't think it is a great idea to discard this approach for the following reasons. First, as the authors have revealed, RBNs preserve some of the important fractal characteristics (i.e., Horton's laws). Therefore, I think a more productive argument would be to clarify in what contexts RBNs are still useful. Second, RBNs may be useful as a NULL model. Since this model lacks a certain aspect of real river networks, comparing the ecological dynamics with RBNs and OCNs may highlight the significance of the fluvial process in natural rivers.

Metapopulation simulation. In my opinion, the ecological models used in this manuscript are oversimplified. Essentially, the authors assumed that population synchrony/colonization dynamics are a direct function of between-patch distance. Under this assumption, metapopulation stability and capacity are merely a simple "transformation" of a distance matrix (of course, the dispersal parameter α plays a role, but it's not important here). Accumulating evidence suggests that population synchrony is not a simple function of between-patch distance in rivers (Larsen et al. 2021, Ecology letters; Peterson et al. 2013, Ecology letters; and many others...). Furthermore, dispersal effects on population synchrony are more complex when accounting for density-dependence in local population dynamics. The authors made a very strong argument on how simple network models can over- or underestimate metapopulation dynamics (e.g., L208-220); however, this argument is too sensitive to the ecological assumptions of a metapopulation model. I strongly encourage the authors to use more sophisticated models to simulate metapopulation dynamics or to explicitly mention the limitations of their analysis.

An alternative measure of "river complexity" in OCNs. I agree that OCNs may best represent real river networks. In the meantime, I wonder what kind of OCN characteristics can be used to measure "river network complexity?" Stream ecologists are very interested in the role of river networks complexity, so a practical guidance on how to measure complexity in OCNs would be very helpful.

Minor comments

L15-17 As I've shown above, it is related to Horton's law. Please see my major comments.

L76-78 Please reconsider this statement in light of my above comment - in my opinion, branching probability is an inherent property of river networks.

L80-82 Please reconsider this statement - this may be true for a specific model the authors used, but not yet sure whether this is a general pattern or not.

L90-91 I'm not sure if I understood this correctly, but the pixel length l of the DEM should not define the extent of a network node - in previous studies, network nodes are determined based on the stream length that corresponds to the scale of a local population or community (see Yeakel 2014, Terui et al. 2018, Terui et al. 2021). It is thus independent of the resolution of the DEM.

L105-116 Even in real river networks, branching probability can be derived by estimating the statistical distribution of the link length x . For example, (1) estimate the rate parameter of link length as $x \sim \text{Exp}(\lambda)$; (2) estimate branching probability P using the CDF of the exponential distribution as $P = 1 - \exp(-\lambda y)$ for a given stream length y (see Terui et al. 2018 and 2021). The method presented in this manuscript (N_L/N) could be misleading because the authors defined the number of network nodes N as the number of pixels of the DEM, not as the number of river sections with an arbitrary length y .

L117-118 Please see my major comment about branching probability.

L121 The parameter A is not defined.

L124-132 My understanding is that the authors mixed the arguments of “physical” and “biological” interpretation of network structure. Branching probability is defined essentially by the rate parameter of an exponential distribution of the link length, which represents the physical property of the river network. How organisms perceive this network structure depends on the organism’s movement scale (I agree with this point), but it does not alter the physical property of the river network per se. If we use the same definition of a node (the spatial scale of a local population/community) and keep an A_T value constant across watersheds, shouldn’t it reflect relative difference in network structure regardless of A_T choice? Excuse me if I misunderstood; I was unsure if I read this paragraph correctly.

L133-140 I agree that an appropriate extraction scale may differ by species; however, it does not alter the relative complexity between river networks. Let say we measured a network structure with a small value of A_T - with this criterion, watershed A had a higher branching probability than watershed B. Therefore, the relative complexity is higher in watershed A than B for a species inhabiting small streams. This “relative complexity” will not change even when we use a larger value of A_T . Watershed A remains more complex than watershed B because it does not change the rate parameter λ .

L149 I think it would be better to represent this result in the abstract more accurately (what characteristics BBTs and RBNs preserve and do not preserve). Also, RBNs are asymptotically identical to Shreve’s random topology model, which is known to have $R_B = 4$ and $R_L = 2$ (Rodriguez-Iturbe and Rinaldo 1997, Fractal River Basins). It would be nice to mention this here.

L157-158 This result has been analytically derived in previous studies (the area scaling exponent equals 0.50 in Shreve’s random topology models; De Vries et al. 1994, Water Resources Research). It would be great to mention this analytical result here.

L167 This is specific to the author’s metapopulation model, not universally true. I would clarify this as “In our definition...”

L175-179 As I mentioned in the major comment, I am not fully convinced that this is a good way to justify their conclusion (BBTs and RBNs overestimate CV_M and underestimate λ_M). In their definition, the metapopulation measures are directly related to distance matrices. I am unsure if this gives any additional information beyond the distance matrix.

L186-187 Please correct me if I misunderstood; does this statement assume the scenario where one may use different A_T values when extracting different river networks? If so, I would never do that when comparing ecological properties across watersheds in relation to network structure. If not, would you be able to elaborate on the issue here?

L191-193 I think this is the original definition of a node in previous studies.

L233-234 “indegree” and “outdegree” may be difficult to interpret for unfamiliar readers. Can you please include brief explanations?

Figure 3c Although the authors showed an “ensemble” pattern of river networks, it would be great if we could see the variation in the area scaling exponent β . I don’t know how variable it is, but I am curious if there are watersheds closer to random constructs (e.g., small or flat watersheds).

Figure 3 & 4 It is unclear how the authors chose the branching probability in these examples - did you choose based on the values of the corresponding OCNs? If so, please clarify in the figure captions.

Reference - The preprint of Terui et al. 2021 has been published here: <https://www.pnas.org/content/118/47/e2105574118>

I hope my comments help improve the manuscript.

Reply to Reviewers

Comments from the Reviewers are in black roman type; our replies are in blue roman type. For cross-referencing, our replies are labelled as **RX**, where X is the progressive reply number.

Reviewer 1

The manuscript by Carraro et al. reviewed methods for river network delineation and pointed to potential problems of a common method - branching probability. The manuscript is very well written and addresses an important topic in stream ecology. I liked the brevity of the manuscript, the beautiful figures, and how they deliver information. However, I am afraid that some of their claims seem to be built upon the misinterpretation of previous research (if I understood their writing correctly). In general, I support the publication of this manuscript, but it would require a substantial reconsideration of the manuscript content.

R1 We wish to thank this Reviewer for the favorable and highly constructive assessment of our work. We especially appreciate the courteous tone of their reply, even when our arguments are in contrast. In the revised version of the manuscript and hereafter we have clarified and justified all our findings, and discussed in more depth the comparison of approaches.

Branching probability. One of the most important findings in this research is that branching probability is not a “scale-invariant” feature of river networks - the authors claimed in L122-123 “branching probability is a non-descriptive property of a river network, which by no means describes its complexity, and depends on the observational scale.” However, I’m afraid I have to disagree with this statement.

R2.1 Many thanks for this detailed reply, which helped us clarify our claims on branching probability. Specifically, we have revisited the wording of our statement, and adjusted where needed, but the main argument—namely that branching probability is “non-descriptive” in the sense that is scale-variant (and thus depends on the grain sizes looked at)—is unchanged. We here briefly summarize the main arguments of our reply, which we will then discuss in detail in the following:

- Branching probability p is not preserved across scales, as opposed to Horton ratios R_B and R_L and the exponent of the power-law scaling of drainage area β . For the same watershed and for a given

cell size l , p decreases as A_T increases (see **R2.3**, **R2.4**).

- p depends on the “ruler” l used to measure the total river network length. For the same catchment and fixed threshold area A_T , p decreases as l decreases (see **R2.3**, **R13**).
- Rivers are not intrinsically characterized by their branching character irrespective of the scale at which they are observed. Different watersheds can rank differently in terms of p when extracted at different A_T values (see **R14**).
- Consequently, using an arbitrary length (e.g., equal to the ecological node size) to determine branching probability is inaccurate (see **R9**, **R10**).

To explain this, let me use the Strahler ordering scheme (this is similar to A_T in terms of “observation scales”). River networks are often claimed as an outstanding example of fractal, and the Horton’s bifurcation/length laws are used as the basis of such a claim. Specifically, the bifurcation/length ratio (R_B and R_L) follows geometric-scaling relationships such that:

$$R_B = N(\omega - 1)/N(\omega); \quad R_L = L(\omega - 1)/L(\omega)$$

where ω is the stream order, and $N(\omega)$ and $L(\omega)$ refer to the number of links and the average length at the order ω , respectively. Here, stream order ω is a resolution-dependent measure because we may find finer 1st order streams as we increase the resolution (smaller A_T value). Nevertheless, the above laws remain valid regardless of the resolution or A_T values, i.e., the limiting channel network is a fractal with properties related to R_B and R_L .

R2.2 We agree with the example provided by the Reviewer on Horton’s laws. R_B and R_L are scale-invariant quantities while stream order ω is a scale-dependent measure.

Branching probability has the same property. Let me assume that the link length follows an exponential distribution with a rate parameter λ . Under this assumption, Packham & Gupta 1999 (Water Resources Research) has shown that the segment length of any stream order ω , L_ω (i.e., from one confluence at which stream order ω begins to another confluence at which stream order $\omega + 1$ begins), will follow an exponential distribution (see equations 17-26 in their paper). More importantly, they found that the cumulative probability distributions of segment length at orders ω and k are identical after simple rescaling as:

$$1 - \exp(-\lambda p_\omega x) = 1 - \exp(-\lambda p_k (R_L^{k-\omega} x)) \quad (\text{R1})$$

where $p_\omega = R_L^{-(\omega-1)}$, λ the rate parameter, and x a given segment length. Note that the above equation

shows the equivalence of branching probabilities measured at different scales - the left side is the branching probability at stream order ω ($Pr(L_\omega < x)$) and the right side is that at stream order k ($Pr(L_k < R_L^{k-\omega} x)$). Therefore, branching probability remains constant across stream orders after multiplicative rescaling. Peckham and Gupta 1999 showed that this statistical self-similarity was indeed observed in natural river networks. While Peckham and Gupta 1999 assumed an exponential distribution for the link length, they also showed that the above result holds true for any statistical distributions in an asymptotic sense.

R2.3 As the Reviewer states, $1 - \exp(-\lambda p_\omega x)$ is the probability that a stream of order ω has length $L_\omega \geq x$. As shown by Peckham and Gupta [1999], this distribution is scale-invariant, i.e. when divided by its mean the distribution maintains the same shape (i.e. remains statistically similar) across different stream orders ω . This is what Eq. (R1) states.

However, the left-hand side of Eq. (R1) depends on x . Hence if, as the Reviewer claims, this were equal to the branching probability, it would mean that branching probability would depend on a length scale x . The quantity that is scale-invariant in Eq. (R1) is R_L ($= 2$ for the Shreve random topology model, as in Peckham and Gupta [1999]—see Eq. 26 therein), not the branching probability. If we assumed that x is the ecological size of a node (i.e. spatial range of local subpopulation) as it seems to be implied, this would mean that different species would perceive different branching probabilities for the same extracted river network (given fixed A_T and l); consequently, branching probability would not be preserved across scales (not even across taxa!). We now added a comment on this aspect (L. 147).

In fact, the left-hand side of Eq. (R1) is not the branching probability. If λ [L^{-1}] is the parameter of the exponential distribution fitted to link lengths, then the branching probability is equal to $1/\lambda$ [L], i.e. equal to the probability that a node is branching, which is given by the number of branching nodes (or branches) N_L divided by the total number of nodes (i.e. the total network length $N_L \lambda$). In this respect, see also **R9** and **R10**. Note that the so-obtained branching probability is dimensional, as λ was dimensional. A proper “ruler” should be used to transform branching probability into a dimensionless quantity. This is why we discuss about the pixel size l in our manuscript.

If I understood correctly, what the authors performed in Fig. 1 is similar to the above exercise - they pruned smaller tributaries from the network by increasing A_T (e.g., removing only 1st order streams) and calculated branching probabilities for the pruned networks. However, their comparison of branching probability is misleading because they did not perform proper rescaling when evaluating statistical similarity across scales. Therefore, in my opinion, their claim is not justified.

R2.4 This is a misunderstanding. Note that Horton’s laws state that bifurcation and length ratios remain constant across scales, that is, for example, $L(\omega = 2)/L(\omega = 1) \approx L(\omega = 3)/L(\omega = 2) \approx \dots \approx R_L$ (the “ $\approx$ ” sign indicates that these relationships are true in a statistical sense). In this case, a given R_L value (same for R_B) defines the topology of a given river network. In particular, being calculated as a ratio,

R_L does not depend on the unit used to measure link lengths. On the contrary, the value of branching probability p does not remain constant across scales, and a single p cannot be associated to a river network regardless of the observational scale. We have revisited the respective paragraph and ensured that our text and argumentation is clear.

Importantly, increasing A_T is actually not exactly equivalent to pruning smaller tributaries from the network; if we increase A_T by one pixel (l^2), all headwater links will reduce their lengths by l , while all other links will not be altered. At the same time, the shortest headwaters (of length l) will disappear from the network; for each such headwater, two links will be removed from the network (i.e., the headwater and the link downstream of it, which will be embedded into the other link upstream). Hence, both N_L and N decrease, but the overall result is a decrease in p_r , as we show in Fig. 2b: the numerator (N_L) decreases more rapidly than the denominator (N).

Furthermore, please note that in our analysis we actually did not evaluate statistical similarity across scales. We would do that if we were interested in studying the distribution of some quantities (e.g. drainage area, longest stream length) as a function of ω . The suggestion implies that, when comparing the same river network extracted with different A_T values, one should adapt the "ruler" length l (which transforms the total river network length into the number of nodes N) so that $p = N_L/N$ would remain constant. As we argued in the above paragraph and in **R2.3**, the scaling of lengths would come into play in the assessment of the similarity of the distributions of stream lengths (Eq. (R1)), not in the assessment of a scale-invariant quantity such as R_L . Our argumentation in the manuscript is much simpler, in that it shows that the branching ratio of a given extracted river network depends on parameters A_T and l , which define the scale at which the network was extracted.

When random river networks can/cannot be used? While I agree that RBNs lack some important characteristics of real river networks (e.g., area scaling), I don't think it is a great idea to discard this approach for the following reasons. First, as the authors have revealed, RBNs preserve some of the important fractal characteristics (i.e., Horton's laws). Therefore, I think a more productive argument would be to clarify in what contexts RBNs are still useful. Second, RBNs may be useful as a NULL model. Since this model lacks a certain aspect of real river networks, comparing the ecological dynamics with RBNs and OCNs may highlight the significance of the fluvial process in natural rivers.

R3 Thanks for raising this point. We agree that RBNs lack some important characteristics of real river networks, and actually this is a major aspect of our argumentation, and the main reason why OCNs produce much more realistic dynamics (e.g. with respect to hydrology, but also metacommunity metrics) compared to any other approaches. Our analysis also shows that RBNs are better than BBTs in reproducing both topology and scaling of real river networks, and metrics of ecological relevance for metapopulations. Yet, we argue that it is not "better than something worse" that should be an argument for a strategy, but "better than

any other approach” that should be our criterion for selection, and with this respect we have showed that OCNs outperform all other approaches, and are by far the best approximation of natural river systems. We do, however, now better acknowledge that there is also a ranking of suitability among the other approaches. Thus, while RBNs prove less accurate than OCNs in reproducing these features of real river networks, their use in modelling works could indeed still be warranted because their generation algorithm is (at least one order of magnitude) faster than that of OCNs, hence they might be used as a null model in cases where a large number of network replicates is required. We expanded on this aspect in the manuscript (LL. 291-297).

Metapopulation simulation. In my opinion, the ecological models used in this manuscript are oversimplified. Essentially, the authors assumed that population synchrony/colonization dynamics are a direct function of between-patch distance. Under this assumption, metapopulation stability and capacity are merely a simple “transformation” of a distance matrix (of course, the dispersal parameter α plays a role, but it’s not important here). Accumulating evidence suggests that population synchrony is not a simple function of between-patch distance in rivers (Larsen et al. 2021, Ecology letters; Peterson et al. 2013, Ecology letters; and many others...). Furthermore, dispersal effects on population synchrony are more complex when accounting for density-dependence in local population dynamics. The authors made a very strong argument on how simple network models can over- or underestimate metapopulation dynamics (e.g., L208-220); however, this argument is too sensitive to the ecological assumptions of a metapopulation model. I strongly encourage the authors to use more sophisticated models to simulate metapopulation dynamics or to explicitly mention the limitations of their analysis.

R4 Thanks for this insightful comment, which prompted us to perform extensive additional and more robust analyses. In addition to the previously used ecological metrics (CV_M and λ_M in the assumption of uniform patch size distribution) we now added a comparison of different network types with respect to two updated metrics $CV_{M,H}$ and $\lambda_{M,H}$ whose calculation includes the effect of non-uniform distribution of patch sizes. Our new results confirm that OCNs are better than RBNs (which in turn are better than BBTs, and we now better state this hierarchy of suitability) in reproducing metapopulation features in real river networks.

Moreover, we agree that, while the distance matrix of a landscape and the distribution of patch sizes have important implications for metapopulation dynamics, other factors such as Euclidean between-patch distance [Larsen et al., 2021], fat-tailed [Muneepeerakul et al., 2008] and density-dependent [Yeakel et al., 2018] dispersal can also play a relevant role. Note also that, in particular with regards to the assessment of the Moran effect in metapopulation synchrony (i.e., increased synchrony in local fluvial populations that are geographically close but not flow-connected [Larsen et al., 2021]), the use of OCNs allows integration of Euclidean distances in a metapopulation model, while this is not possible for RBNs and BBTs, where Euclidean distances are not defined. We added a paragraph where we discuss these aspects specifically

(LL. 271-285).

An alternative measure of “river complexity” in OCNs. I agree that OCNs may best represent real river networks. In the meantime, I wonder what kind of OCN characteristics can be used to measure “river network complexity?” Stream ecologists are very interested in the role of river networks complexity, so a practical guidance on how to measure complexity in OCNs would be very helpful.

R5 This is also a good suggestion. We now commented on the fact that studies exploiting synthetic river networks should always clarify the scales (total area drained, size of a node, area drained by a headwater) that the synthetic networks subsume. Only in such a way could the predictions from these studies be compared with the reality (LL. 296-300).

Minor comments. L15-17 As I’ve shown above, it is related to Horton’s law. Please see my major comments.

R6 Please refer to our main replies **R2.3** and **R2.4**.

L76-78 Please reconsider this statement in light of my above comment - in my opinion, branching probability is an inherent property of river networks.

R7 We respectfully disagree, as this is a property that is directly depending on the scale the network is assessed, and thus it is scale-variant. See our previous replies and our formal argumentation of why this is so.

L80-82 Please reconsider this statement - this may be true for a specific model the authors used, but not yet sure whether this is a general pattern or not.

R8 Thanks. We now corroborated our results with the addition of metrics $CV_{M,H}$ and $\lambda_{M,H}$ that depend both on the distance matrix and on patch-size distribution. We acknowledged that our results depend on these characteristics of river networks (L. 86).

L90-91 I’m not sure if I understood this correctly, but the pixel length l of the DEM should not define the extent of a network node - in previous studies, network nodes are determined based on the stream length that corresponds to the scale of a local population or community (see Yeakel 2014, Terui et al. 2018, Terui et al. 2021). It is thus independent of the resolution of the DEM.

R9 Indeed, this is the definition of node size in an ecological sense, as we state later on in the manuscript

(LL. 138-140). However, river networks are extracted following geomorphological principles, and the total river network length (equal to the number of nodes N if measured in terms of the node size l , whatever the definition of a node is) will depend on the resolution at which the river network is extracted. In this paragraph, we explain how river networks are extracted “*from a geomorphological perspective*” (L. 94). We now expanded the beginning of this paragraph to clarify that geomorphological and ecological definitions of a node are generally discordant (LL. 93-94).

In addition, please note that using the ecological definition of node size to measure total river length (and hence N) is problematic. Indeed, if for instance we assume that the local population range is 1 km, we do not know how to treat all tributaries whose length is < 1 km. Given the assumption of exponential distribution of link lengths with mean length $1/\lambda$ [km], there will be many links much shorter than the assumed node length (the probability that a link has length < 1 km is $1 - \exp(-\lambda)$). A similar issue occurs for all other links, as their length would need to be rounded to the nearest integer (in km, if $l = 1$ km). If all link lengths are rounded up, then the transformed link length will follow a geometric distribution with rate $1 - \exp(-\lambda)$ (indeed, if X is a continuous random variable such that $X \sim \text{Exp}(\lambda)$, then $\lceil X \rceil \sim \text{Geometric}(1 - \exp(-\lambda))$). If this is the reason why the Reviewer proposes $1 - \exp(-\lambda)$ as an estimate of branching probability for real rivers (see also **R10**), we observe that this formula is inaccurate because of the rounding operation, all the more the larger l is (i.e., the larger the range of a local population). We added a comment on this aspect in the manuscript (LL. 148-153).

Finally, we observe that it is indeed possible to run metapopulation models by using the DEM pixel as a node, provided that this is smaller than the local extent of a population. Indeed, increasing the spatial resolution of a model is never a problem per se (barring overfitting issues, which are out of scope here).

L105-116 Even in real river networks, branching probability can be derived by estimating the statistical distribution of the link length x . For example, (1) estimate the rate parameter of link length as $x \sim \text{Exp}(\lambda)$; (2) estimate branching probability P using the CDF of the exponential distribution as

$$P = 1 - \exp(-\lambda y) \tag{R2}$$

for a given stream length y (see Terui et al. 2018 and 2021). The method presented in this manuscript (N_L/N) could be misleading because the authors defined the number of network nodes N as the number of pixels of the DEM, not as the number of river sections with an arbitrary length y .

R10 The approach proposed is problematic for two reasons. First, defining branching probability for real rivers via Eq. (R2) means that p depends on an arbitrary length y . We do not see how a quantity dependent on an arbitrary length could be preserved across scales. Note that, for example, Horton’s length ratio R_L is defined irrespective of a length scale. Second, if y is to be assumed as the range of a local population (node in the ecological sense), problems arise in the treatment of links with length $< y$ (see **R9**).

We hope that the following example will clarify our point. Let us consider the schematic RBN in Fig. 1 of Terui et al. [2018] (here reproduced in Fig. 1b), which has 15 links and 30 nodes, hence $p = 0.5$. Let us assume that that network is a real river network, where each link has length equal to 1 km. Fitting an exponential distribution to the link lengths is equivalent to equalizing their means: $1/\lambda = 30/15$ km, hence $\lambda = 0.5 \text{ km}^{-1}$. λ is dimensional, as it depends on the node size; if we measure $1/\lambda$ in units of $l = 1$ km, we have $\lambda = p$ (here l is the “ruler” used to measure river network length; in this case of course every link will contain an integer number of l ’s). If we defined branching probability via Eq. (R2) with $y = l$ (i.e. the arbitrary length is set equal to the node size, with no distinction between a “geomorphological” and an “ecological node size” here), this would be equal to $1 - \exp(-0.5) = 0.393$, which is different than the value $p = 0.5$ indicated in Fig. 1 in Terui et al. [2018]. We hence conclude that the correct measure for branching probability in real river networks is $p = N_L/N$, where N is the number of units l used to measure the river network length.

L117-118 Please see my major comment about branching probability.

R11 Please refer to our replies **R2.3**, **R9** and **R10**.

L121 The parameter A is not defined.

R12 We revised the text and ensured that A is defined (L. 98).

L124-132 My understanding is that the authors mixed the arguments of “physical” and “biological” interpretation of network structure. Branching probability is defined essentially by the rate parameter of an exponential distribution of the link length, which represents the physical property of the river network. How organisms perceive this network structure depends on the organism’s movement scale (I agree with this point), but it does not alter the physical property of the river network per se. If we use the same definition of a node (the spatial scale of a local population/community) and keep an A_T value constant across watersheds, shouldn’t it reflect relative difference in network structure regardless of A_T choice? Excuse me if I misunderstood; I was unsure if I read this paragraph correctly.

R13 Indeed branching probability is defined by the rate parameter of an exponential distribution (see **R10**), i.e. the mean link length. This does not change for different species with different spatial ranges, but it does change depending on the “ruler” used to measure river network lengths (in analogy with the example of the length of the coast of Britain from Mandelbrot [1967]). By following the Reviewer’s argument, if different species have different “ecological node sizes”, then the river length value used in Eq. (R2) will be different, and so would be p according to that formula. See **R14** with respect to relative differences in network structure.

L133-140 I agree that an appropriate extraction scale may differ by species; however, it does not alter the relative complexity between river networks. Let say we measured a network structure with a small value of A_T - with this criterion, watershed A had a higher branching probability than watershed B. Therefore, the relative complexity is higher in watershed A than B for a species inhabiting small streams. This “relative complexity” will not change even when we use a larger value of A_T . Watershed A remains more complex than watershed B because it does not change the rate parameter λ .

R14 We thank this Reviewer for this comment, which prompted us to conduct an additional analysis (see Fig. 3) in which we show how branching ratio p_r varies across A_T values for the 50 real river networks analyzed. We found that the ranking of p_r values across rivers is not respected for different A_T values: a river that looks more branching (i.e., has higher p_r) than other rivers at a high resolution (low A_T) might be less branching than other rivers at low resolution (high A_T).

L149 I think it would be better to represent this result in the abstract more accurately (what characteristics BBTs and RBNs preserve and do not preserve). Also, RBNs are asymptotically identical to Shreve’s random topology model, which is known to have $R_B = 4$ and $R_L = 2$ (Rodriguez-Iturbe and Rinaldo 1997, Fractal River Basins). It would be nice to mention this here.

R15 We mentioned this aspect as suggested (LL. 183-186).

L157-158 This result has been analytically derived in previous studies (the area scaling exponent equals 0.50 in Shreve’s random topology models; De Vries et al. 1994, Water Resources Research). It would be great to mention this analytical result here.

R16 We mentioned this aspect as suggested (LL. 183-186).

L167 This is specific to the author’s metapopulation model, not universally true. I would clarify this as “In our definition...”

R17 Thanks for this pertinent comment. The whole paragraph has been revised following the introduction of $CV_{M,H}$ and $\lambda_{M,H}$ metrics.

L175-179 As I mentioned in the major comment, I am not fully convinced that this is a good way to justify their conclusion (BBTs and RBNs overestimate CV_M and underestimate λ_M). In their definition, the metapopulation measures are directly related to distance matrices. I am unsure if this gives any additional information beyond the distance matrix.

R18 We now included additional metrics $CV_{M,H}$ and $\lambda_{M,H}$, which depend on a non-uniform patch size distribution, as well as on the distance matrix of a landscape. See **R4** for details.

L186-187 Please correct me if I misunderstood; does this statement assume the scenario where one may use different A_T values when extracting different river networks? If so, I would never do that when comparing ecological properties across watersheds in relation to network structure. If not, would you be able to elaborate on the issue here?

R19 Thanks for raising this important point, which helped us clarify our reasoning. As we have shown in our manuscript, branching probability is not a property that describes the branching character of a river. Instead, p is a feature that depends at the scale at which a river network is observed. With our additional analysis (see **R14** and Fig. 3), we now show that the ranking of real rivers used in this analysis in terms of p changes as the threshold area A_T changes.

Note that our analysis was focused on the case where real rivers of different sizes (i.e., catchment area in km^2) were compared by discretizing their surface into pixels of different sizes l , such that the total number of pixel was similar (around 40,000). When we fixed, say, $A_T = 100$ pixels (the same would occur for the other values used), we implied that the value of A_T in km^2 scaled with l , so that $A_T[\text{km}^2]/A[\text{km}^2]$ was approximately constant. If one compares different river networks spanning different catchment areas (in km^2), all of them extracted from the same DEM (same l and same A_T in km^2), then the larger river network will appear more branching (i.e., have larger p_r). Indeed, by selecting catchments with larger A in km^2 for fixed l and A_T in km^2 , one moves towards the top-left corner of Figs. 2a,b (i.e., perpendicular to the level curves A_T/A). We now comment on this aspect in the manuscript (LL. 225-232).

L191-193 I think this is the original definition of a node in previous studies.

R20 This depends on whether the viewpoint on the river network structure is “geomorphological” or “ecological” (see also **R9**). We now expanded the initial paragraph of the section (LL. 93-94) to ensure that this distinction is clearer.

L233-234 “indegree” and “outdegree” may be difficult to interpret for unfamiliar readers. Can you please include brief explanations?

R21 We added references to the glossary.

Figure 3c Although the authors showed an “ensemble” pattern of river networks, it would be great if we could see the variation in the area scaling exponent β . I don’t know how variable it is, but I am curious if there are watersheds closer to random constructs (e.g., small or flat watersheds).

R22 This is an interesting suggestion. We added a Supplementary Table (Table S1) providing values of Horton ratios R_B , R_L and exponent β of the power-law scaling of drainage areas fitted separately for each

of the 50 real rivers used in the analysis. Moreover, we added Supplementary Figure S3, where we show that these β values are correlated with total drainage area expressed in number of pixels; this shows that the watersheds whose scaling exponent is closer to the mean-field value 0.5 [Rinaldo et al., 2014] are those that were more coarsely extracted. Indeed, our choice of setting $A = 40,000$ pixels $\pm 20\%$ was dictated by a trade-off between accuracy in estimating scaling features of rivers (which would require highly resolved DEM data) and computational effort to generate and analyze synthetic networks of analogous size.

Figure 3 & 4 It is unclear how the authors chose the branching probability in these examples - did you choose based on the values of the corresponding OCNs? If so, please clarify in the figure captions.

R23 We added a reference to the Methods in these captions, where the derivation of real and synthetic river networks is detailed.

Reference - The preprint of Terui et al. 2021 has been published here: <https://www.pnas.org/content/118/47/e2105574118>

R24 Thanks, we updated the reference.

Reviewer 2

Thank you for the opportunity to review this manuscript. The authors argue that Optimal Channel Networks (OCN) create realistic representations of river networks and can more accurately capture metapopulation properties than random branching networks (RBN) and balanced binary trees (BBT). Overall, I found these arguments to be well supported and believe this paper makes a valuable contribution to increasing our theoretical understanding of riverine metapopulations. Before publication however, I have some minor recommendations for the authors.

R25 Thanks for the favorable assessment of our manuscript. We have addressed and incorporated all suggestions.

Figure1: Include an OCN network adjacent to BBT and RBN with similar parameter values in top row. It was difficult to understand how A_T values were used to standardize/compare networks since BBT and RBN are not related to area. An additional panel should help readers understand that N can be extracted from an OCN (with an A_T) and used to create comparable BBT and RBN (before reading the methods).

R26 Thanks for this good idea. We revised Figure 1 as suggested by the Reviewer (see new panel c).

Line 73: Typo. “functional” should be “function”

R27 We have revisited this sentence, but respectfully decided to keep it unchanged, as “functional” is the appropriate term for a function that maps a vector space (drainage area A_i for all cells i) into a field of scalars (total energy expenditure). As such, this term has also been consistently used in OCN literature [Rinaldo et al., 1998; Rodriguez-Iturbe and Rinaldo, 2001; Rinaldo et al., 2014], and it would be important to keep the use of this terminology constant.

Line 107-113: Consider adding an image of an artificial network labeled with terms in glossary (links, nodes, confluences, etc.). A supplementary figure would complement the existing definitions and eliminate any misunderstanding regarding the derivation of P_r . For example, to understand P_r the reader needs to know that a link is between confluences (or a source and confluence) and not between two nodes (as it is sometimes defined).

R28 Thanks for this good suggestion. We added a supplementary figure (Fig. S11) that further clarifies the main technical terms used in the manuscript.

Line 124: “scale dependency” is better than “problem of scaling”. I do not think scaling is a problem per se. The problem is more that metrics can change with scale of observation (see figure 1 in Jackson and Farhig 2015. Global Ecology and Biogeography for a conceptual diagram). Scaling only becomes a problem when the change is not predictable.

R29 We very much agree with this comment. We revised the text and used the term “scaling” rather than “problem of scaling”.

Line 126-132: I found it confusing that the paragraph above dismisses P_r for being scale dependent while this paragraph recognizes scale dependence is ubiquitous and important. Thus, it seems like P_r can be both undesirable and desirable because of scale dependency? If this was not the intended interpretation, changing the order of the paragraphs may help clarify.

R30 Thanks for this comment. Please note that we do not want to say or imply that p_r is either good or bad. As we show in the previous paragraph, p_r is a feature of a river network that depends on the scale(s) used to extract the river network (A_T and l). It can be used to characterize a river network at a given observational scale, but it will not be preserved if the observational scale changes. In this paragraph, we highlight that one needs to be careful about the concept of scaling (and the definition of the size of a node) when extracting a river network for ecological studies. As a concluding remark, we now state that researchers dealing with synthetic networks should always clarify the observational scales that their networks embed (LL. 297-301).

Line 142, 156: Provide more detail regarding power-law scaling as it pertains to Figure 3c. This would fit well with the text explaining 3a and 3b in the supplement. Specifically, describe the salient features of “ $P[A > a]$ as a function of a ” from the citations provided. This should help the reader better understand the scaling results.

R31 This is a pertinent comment. As suggested by the Reviewer, we expanded the text in the Supplementary Information that clarifies technical details of this Figure and implications of the power-law scaling of drainage areas.

Line 168: How were connectivity patterns chosen? Clarify that the different methods used to create artificial stream networks produce different connectivity patterns.

R32 We now revised the whole paragraph, given that we added metrics $CV_{M,H}$ and $\lambda_{M,H}$ to our analysis.

Line 216: “Correct ecological conclusions” may be too strongly worded because this study was mostly theoretical. I think it would be better to state that OCN produce conclusions that are consistent with those obtained from real stream networks (which may or may not be “ecologically correct”).

R33 We agree. We now rephrased as “*conclusions that are in line with those that could be observed in real river networks*” (L. 289)

Line 220: If possible, a discussion, either here or in the introduction (Line 54), outlining the specific stream network attributes OCNs allow us to generalize and how this helps us understand the ecology of real stream networks would be valuable. Since it is becoming rather routine to extract real river networks from either digital elevation models or digital flowlines, why not use real stream networks or the geometry directly measured from them for analysis?

R34 We added a sentence in the introduction that discusses the importance of generating replicates of river network analogues with the same properties in ecological modelling studies (LL. 55-58). We also added a paragraph in the discussion where we more specifically discuss about the roles of distance matrix and patch-size distribution in determining metapopulation attributes of a landscape (LL. 246-270).

Line 278: Correct citation to (Zimmerman and Ver Hoef, 2017)

R35 Thanks for spotting this. We corrected the reference.

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22nd Feb 22

Dear Dr Carraro,

Your manuscript titled "The structure of dendritic river networks shapes ecological dynamics" has now been seen by 2 reviewers, whose comments are appended below. In the light of their advice I regret to inform you that we cannot publish your manuscript in Communications Earth & Environment.

We note that both reviewers continue to see interest in your analysis and that Reviewer #2 is satisfied with your responses to their previous comments. However, Reviewer #1 raises some seemingly important and recurrent concerns. We are particularly concerned by the points raised regarding metapopulation simulation and the assumptions therein. In light of these concerns, specifically, we remain unconvinced that you have provided sufficient evidence that Optical Channel Networks outperform other synthetic network analogues in estimating ecologically relevant, real river metapopulation parameters. Unfortunately, we are therefore unable to conclude that your manuscript provides the kind of advance, for example beyond your earlier work (e.g. <https://doi.org/10.1002/ece3.6479>), that would be appropriate for publication in Communications Earth & Environment. We are committed to providing a fair and constructive peer-review process. Please feel free to contact us if you wish to discuss our decision in more detail.

I am sorry that we cannot be more positive on this occasion and thank you for the opportunity to consider your work.

Best regards,

Dr Clare Davis
Senior Editor
Communications Earth & Environment

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Reviewers' comments:

Reviewer #1 (Remarks to the Author):

Thank you so much for addressing my concerns. I appreciate the time they have taken for this revision. I have reviewed this manuscript carefully again. First of all, I have to admit that I am not a "true" expert of this research area; I have not been trained formally (I taught myself through readings) nor worked with geomorphologists so far. Hence it is certainly possible that my comments are entirely wrong. If this is the case, please let me know and I'd be happy to communicate with the editor. However, although my knowledge in this field is limited, I believe the following points are worth of further consideration.

According to Rodriguez-Iturbe and Rinaldo 2001, scale invariance is defined as "...The concept of

fractals...characterizes those objects in which properly scaled portions are identical...to the original object. In river basins, we will always deal with the statistical description of components and thus the 'fractal' scaling property refers to the invariance of the probability distributions describing the object's composition under geometric transformations or changes of scale." - p. 99 in Rodríguez-Iturbe and Rinaldo (2001). From my reading (my apologies if this is my misunderstanding), it sounded like the authors referred to scale invariance as a geometric scaling factor or scaling exponent per se, such as Horton's R and beta (because they are constant; please see my detailed comment why they are constant across scales). If this is the case, I don't believe this is a common definition of scale invariance - the definition presented above is more common (and correct, I believe) in statistics, mathematics, and geomorphology.

If my argument (detailed in the attachment) is correct, this undermines the major conclusion of this manuscript. I appreciate it if the authors could carefully consider my points.

Akira Terui
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Reviewer #2 (Remarks to the Author):

I believe that the authors addressed all concerns mentioned in the initial review and am satisfied with the revised version of this manuscript.

I support its publication.

Review of manuscript by Carraro and Altermatt

Akira Terui

Thank you for addressing my comments. The authors did a great job in clarifying some parts of the manuscript, and I have a better understanding of the manuscript content. However, I'm afraid that the revised manuscript does not address some of my major concerns (I simply have a different opinion on this topic). I described my concerns below.

Metapopulation simulation

I appreciate that the authors included the variation in habitat size in their simulation, and I agree that OCNs have a better extension capacity (e.g., the inclusion of Euclidean distance).

However, my primary concern was how they modeled population synchrony, not habitat size. As I wrote in the previous round of review, the authors made an assumption that population synchrony in the metapopulation CV model decreases with distance (and **deterministic!**) and implied such synchrony is caused exclusively by dispersal (the model itself does not assume the dispersal is the sole cause, but author's interpretation does; L362-363). This is a very strong assumption, requiring extensive support from the literature. However, this is not the case. First, dispersal is not the sole cause of population synchrony. Moran effects, predators, and many other factors contribute to population synchrony because population synchrony is merely a statistical correlation of two population time series (phenomenological). Therefore, it is inappropriate to describe "... α a parameter expressing the mean dispersal distance." A more accurate description would be "... α is the parameter defining the distance decay of population synchrony..." Second, and more importantly, distance dependence in population synchrony is not well supported in rivers. For example, the population synchrony of salmons within a single watershed shows a vague relationship with river distance (Braun et al. 2016; Koizumi et al. 2008; Rogers and Schindler 2008). Therefore, expressing population synchrony as a direct function of distance is ecologically unrealistic given the exclusive focus of this study on rivers (distance dependent synchrony may be appropriate in 2D systems though).

A fair comparison of metapopulation CV with different river metrics (BBT, RBN, and OCN) would therefore need "bottom-up" modeling, where local population dynamics (e.g., Beverton-Holt with density-dependent terms in population growth), environmental stochasticity and similarity, and dispersal (inter-patch movement of individuals) are explicitly modeled. Population synchrony should be treated as the emergent property of these ecological processes. In my previous simulation, in which I modeled these processes explicitly, the distance dependence in population synchrony did not appear (at least, very vague) in simulated river networks (see SI in (Terui et al. 2018)).

I am not suggesting that the authors must re-perform the analysis (because their focus is not ecological modeling *per se*). However, the authors should mention how the violation of distance-dependent synchrony would affect the simulation results (which is often true in rivers). Under the author's metapopulation model, I anticipate there will be a less (and perhaps negligible) difference among BBT, RBN, and OCN with a noisy or no distance dependence in population synchrony.

Please note that the distance dependence assumption would be reasonable in the case of metapopulation capacity because it deals with colonization, which may be tightly linked to dispersal (clearly distance-dependent) in most scenarios.

Scale invariance

Thank you for addressing my concerns. I appreciate the time the authors have taken for this. However, I feel there is miscommunication - partly because of my unclear wording. To avoid further miscommunication, let me define the following terms in analog of structural and functional connectivity:

Term	Interpretation
Structural complexity	Geomorphological complexity of branching pattern of a river network - this measure purely reflects physical properties of rivers, and the perception of organisms is not relevant for this measure
Functional complexity	Ecological complexity of branching pattern that considers the perception of organisms. Different organisms view the same river network differently.

Also let:

Term	Interpretation
u	Given river distance to measure branching probability. Interpretation includes, but not limited to, an “ecological” ruler defining the scale of a population/community. Dimensional.
l	DEM pixel size (length of a side). Dimensional.
A	Entire watershed area. Dimensional.
A_T	Threshold value of watershed area that initiates river lines. Dimensional.
λ	Rate parameter of an exponential distribution for link length. Dimensional.
L	Length of an individual link (random variable). $L \sim Exp(\lambda)$. Dimensional.
L_{total}	Total river length. Dimensional.
N_L	Number of links.
N_{pixel}	Number of river DEM pixels with length l .
N	Number of nodes with length u . Branching or upstream terminal sections ($< u$) still represent one “section” as a node.
p	Theoretical branching probability in a discretized river network.
p_b	Empirical branching probability for a given river length u , $1 - exp(-\lambda u)$. Dimensional.
p_r	Branching ratio N_L/N , as defined by the authors.

Issue of structural complexity

Link length distribution. Before the main point, please allow me to clarify the definition of “scale invariance” - I think the authors understand it (likely than I do), so the following explanation is meant just to clarify the argument. I believe scale invariance refers to

... The concept of fractals... characterizes those objects in which **properly scaled portions are identical... to the original object**. In river basins, we will always deal with the statistical description of components and thus **the ‘fractal’ scaling property** refers to **the invariance of the probability distributions** describing the object’s composition under geometric transformations or changes of scale. (*emphasis added*) - p. 99 in Rodríguez-Iturbe and Rinaldo (2001).

In the following, I refer to scale invariance as the invariance of the probability distributions (or functions) across scales after proper rescaling (see also p.146 in Rodríguez-Iturbe and Rinaldo 2001 for self-affine process, which has different scaling exponents for different axes). In line with this definition, the following function has a feature of scale invariance:

$$f(\psi x) = \psi^z f(x) \quad (\text{S.1})$$

where ψ is the scaling factor. A power law function would be the most famous example:

$$y \approx f(x) = kx^z \quad (\text{S.2})$$

$$y \approx f(\psi x) = k(\psi x)^z = \psi^z kx^z = \psi^z f(x) \quad (\text{S.3})$$

where z is the scaling exponent, k the scaling constant. Now, let me speak about the property of *link length*. The rate parameter for the link length distribution λ follows a power-law of A_T , as shown by the authors (equation (1) in the main text):

$$E(p_r) = \lambda \approx kA_T^z \quad (\text{S.4})$$

Please note that I ignored the term $A^{-0.032}$ in equation (1) because A is constant when evaluating scale invariance in a given watershed with a fixed pixel size l . Also, $E(p_r) = \lambda$ was shown by the authors - see R.2.3 in their response letter (they wrote $p_r = 1/\lambda$, but I think this is an error. . . the mean link length is λ^{-1} , so $p_r = \frac{N_L}{N} = \frac{N_L}{N_L \lambda^{-1}} = \lambda$). The λ becomes a constant across A_T after proper scaling

$$\lambda' = \frac{\lambda}{A_T^z} \approx k \quad (\text{S.5})$$

The part and the whole look alike. I did a poor job in explaining what the “proper rescaling” meant, but what I meant was the rescaling of the rate parameter by A_T or stream order, not changing l subjectively (if we do this, any statistical quantity can be constant across scales. . . obviously inappropriate). Along this line, if we compare λ at $A_T = a_1$ and a_2 (λ_{a_1} and λ_{a_2} , respectively), the two becomes identical after simple scaling:

$$\lambda_{a_1} = \left(\frac{a_1}{a_2}\right)^z \lambda_{a_2} \quad (\text{S.6})$$

Peckham and Gupta (1999) proved that, if link length L measured at one specific *discrete* scale (i.e., stream order ω) follows an exponential distribution, then the link length measured at another *discrete* scale also follows an exponential distribution with a different mean (but the mean changes predictably). Given that $z = -\frac{\log R_L}{\log R_A}$ ($R_A = A_T(\omega + 1)/A_T(\omega)$), a similar phenomenon should occur across *continuous* scales A_T ; indeed, the link length distribution followed an exponential distribution regardless of A_T in Hokkaido, Japan (**Figure 1**). Therefore, the “rescaled,” non-dimensional link length $L' = L/A_T^z$ (random variable) suffices the following equation:

$$L' \sim \text{Exp}(\lambda') \quad (\text{S.7})$$

Alternative expression would be:

$$L_{a_1} \stackrel{d}{=} \left(\frac{a_2}{a_1}\right)^z L_{a_2} \left(\approx \frac{\lambda_{a_2}}{\lambda_{a_1}} L_{a_2}\right) \quad (\text{S.8})$$

where $\stackrel{d}{=}$ indicates the equality in probability distribution. In this example, the scaling factor is the ratio of A_T : $\psi = \frac{a_2}{a_1}$. Therefore, the rate parameter and associated distribution change predictably across scales, and such geometric transformation is defined by the ratio of A_T and the exponent z .

To confirm the above argument, I extracted stream networks of 197 watersheds in Hokkaido, Japan, with 10 values of A_T (MERIT Hydro was used for extraction (Yamazaki et al. 2019)). I estimated the rate parameter at each extraction scale ($A_T = 1, 2, 3, \dots, 10 \text{ km}^2$). Then, the following model was fitted to the data to estimate the scaling exponent and constant for watershed j :

$$\ln \lambda_i \sim \text{Normal}(\mu_i, \sigma^2) \quad (\text{S.9})$$

$$\mu = \ln k_{j(i)} + z_{j(i)} \ln A_{T,i} \quad (\text{S.10})$$

In this model, I allowed $\ln k_j$ and z_j to vary by watershed (i.e., random intercept and slope) so that I can estimate watershed specific values. We estimated the rescaled rate parameter $\hat{\lambda}'$ based on the estimated z and the rate parameter λ_1 estimated at $A_T = 1 \text{ km}^2$ ($\hat{\lambda}' = \frac{\lambda_1}{A_T^z}$). As expected, the estimated $\hat{\lambda}'$ was consistent with k and did not show systematic changes across scales at all the watersheds (**Figure 2**; fluctuations may be caused by statistical uncertainty). In addition, λ_1 and the scaling constant k were closely associated (Spearman's rank correlation = 0.83, $n = 197$), two parameters that should in theory be identical in the absence of statistical uncertainty (see **Equation S.5**). The high correlation of these two parameters indicates that the rate parameter estimated at one specific scale can represent the rate parameters measured at other scales (statistically speaking, k is the geometric mean of rescaled rate parameters λ' across scales).

The above exercise is essentially the same as what I presented in the previous round of review - in the last comment, I used the Strahler ordering scheme to make the argument simple. The only difference is whether the observation scale is expressed in a *discrete* (stream order) or *continuous* form (A_T). If we use the Strahler order (denoted by ω and ξ) instead of A_T , then it becomes (equation 26 in Peckham and Gupta (1999)):

$$L_\omega \stackrel{d}{=} R_L^{\omega-\xi} L_\xi \quad (\text{S.11})$$

where R_L is Horton's length ratio, which is defined by the average link length (= the inverse of rate parameter λ^{-1}) at two consecutive stream orders:

$$R_L = \frac{\lambda_{\omega+1}^{-1}}{\lambda_\omega^{-1}} = \frac{\lambda_\omega}{\lambda_{\omega+1}} \quad (\text{S.12})$$

In this sense, I noted in the last review as "...what the authors performed in Fig. 1 is similar to the above exercise - they pruned smaller tributaries from the network by increasing A_T ." Both exercises follow the same principle, and the multiplication of a common factor (either $(\frac{a_2}{a_1})^z$ or $R_L^{\omega-\xi}$) leads to the invariance of the link length distribution across scales. As I noted above, z is a function of R_L ($z = -\frac{\log R_L}{\log R_A}$).

The authors claimed that λ (and hence, branching probability) changes with A_T , and this is the main reason why this metric is not an inherent property; however, I am not saying that each river network has a *unique* λ without rescaling (and no measurable, dimensional quantity satisfies this condition...I believe...). What I am saying is that the rate parameter λ (and therefore the distribution of link length) is a statistical quantity derived from a fractal scaling property of river basins.

While λ' is independent of R_L , it is important to note that R_B is a function of λ' and R_L , at least in random topology models. Peckham (1995) (see equation 6) has derived the following equation based on Tokunaga's model:

$$R_B = \frac{(2 + \lambda' + R_L) + [(2 + \lambda' + R_L)^2 - 8R_L]^{\frac{1}{2}}}{2} \quad (\text{S.13})$$

It is clear from this equation that R_B is an increasing function of λ' (in equation 6 in their paper, notice that $a = \lambda'$ and $c = R_L$). Indeed, R_B was positively associated with λ' in Hokkaido (**Figure 3**).

From my reading (my apologies if this is my misunderstanding), it sounded like the authors referred to scale invariance as a geometric scaling factor or scaling exponent *per se*, such as R_L and z . If this is the case, I don't believe this is a common definition of scale invariance - the definition presented above is more common (and correct, I believe) in statistics, mathematics, and geomorphology. The constant values of R_L and z emerge as a result of statistical self-similarity (see *Horton's law and statistical similarity*). They are already "properly scaled" quantities by taking a ratio of dimensional quantities of consecutive stream orders (in response to the author's claim in R2.4).

Branching probability. Let me define branching probability as $p_b = 1 - \exp(-\lambda u)$ for now (see section *Branching ratio* for more discussion). Assuming the above argument is correct, the rescaled, non-dimensional rate parameter characterizes the structural complexity of a river network across scales. The rescaled branching probability $p'_b = 1 - \exp(-\lambda' u')$ is therefore non-dimensional and constant across scales (at least, in theory). Note that the length scale used to measure branching probability (u') becomes non-dimensional because it is measured in the unit of λ' .

As far as we are concerned about *structural complexity*, there is no need to define the scale of population/community, and the rescaled branching probability simply means the probability of $L' < u'$. For this reason, I still think branching probability is a reasonable measure to approximate environmental heterogeneity or any other factors related to branching patterns.

Issue of ecological complexity

Yet, the use of branching probability would be complicated when it comes to "*ecological complexity*." We need to define an ecologically relevant "characteristic scale," and different species may recognize the same (rescaled) branching probability differently. However, I don't believe this is a problem *unique* to branching probability because R_B is a function of λ' . For example, species that prefer smaller tributaries may benefit from higher R_B , but species that prefer larger streams may not, as noted by the authors (L.154-161). Therefore, different species will recognize the same value of R_B (and R_L) differently. Also, recall that R_B and R_L defines the scaling exponent of watershed area ($\beta = 1 - \frac{\log R_L}{\log R_B}$) and fractal dimension D ($D = \frac{\log R_B}{\log R_L}$) (p.143 in Rodríguez-Iturbe and Rinaldo (2001)). Thus this argument is pertinent to all the other metrics.

I understand the author's claim that *organism's perception is dimensional*, and I totally agree with this point. However, if this is a problem to branching probability, then it is a problem for other measures of fractal scaling properties too. Once we consider the influence of fractal properties on species, the organism's perception plays a role, and the resultant outcome is no longer non-dimensional (because we have to think about *fractal measures relative to the organism's perception*).

Therefore, the point raised by the authors is not a problem unique to branching probability. It is a problem with all the fractal scaling properties of rivers.

Branching ratio

Thank you for the detailed explanation. I was implicitly assuming $u > l$ in my comment, and it has caused confusion. My apologies. The following is not a comment requesting a revision, but let me clarify the miscommunication regarding the relationship between p_r and $p_b (= 1 - \exp(-\lambda u))$. My understanding is that the authors intended to provide a proxy of branching probability that is measurable in real river networks so that theoretical branching probability $p \approx p_r$. Mine too.

To give an example, let me assume the DEM with pixel size l is acceptably accurate [$l = 0.03$ km, for example], such that the "true" total river length equals the number of river DEM pixels ($L_{total} [pixel] \approx N_{pixel}$). Also, I assume a single value of A_T , as it does not change the following argument. Assuming $u > l$ (e.g., $u = 100 [pixel]$), defining branching probability as $p_r = \frac{N_r}{N}$ means that river sections shorter than u represent branching nodes (therefore, $uN > N_{pixel}$). The same quantity can be measured differently. Using the accurate

river network, we can estimate the average link length $\lambda_{pixel}^{-1} [pixel]$ by assuming the link length $L [pixel]$ follows an exponential distribution. Then, $p_r = \frac{N_L}{N} = 1 - \exp(-\lambda_{pixel}u) = p_b$ or $\lambda_{pixel} = -\ln(1 - p_b)$ because both metrics assume that a river section with $< u$ represents one branching node. I agree with the ecological problem of this definition.

In the meantime, in R2.3, the authors state “... the left side of Eq. (1) is not the branching probability...” and wrote $p_r = \frac{N_L}{N_L \lambda^{-1}} = \lambda$. This equation holds true only when $u = l$ because it assumes $N_L \lambda^{-1} = N_{pixel} = N$ in the denominator. As $l \rightarrow u$, the number of nodes within each link (= link length $L[node]$) will decrease such that $\lambda_{node}[node] = p_r = 1 - \exp(-\lambda_{pixel}u)$, where $L[node] \sim \text{Exp}(\lambda_{node})$. So, what I suggested is identical to author’s metric when $u > l$. When I extract river networks, I often use resolutions that are fine enough to capture headwater tributaries (e.g., 30m or 90m) - so $u > l$ was always the case. I think our metrics are compatible - just a different assumption.

Example:

```
# "true" link length distribution
lambda <- 0.5
n_link <- 1000
x <- rexp(n_link, rate = lambda)

# fitting exponential to true link length
est1 <- fitdistrplus::fitdist(x, "exp")
lambda_pixel <- est1$estimate

# discretize by u; assuming u >> l
# fitting exponential to link length measured in number of nodes with length u
u <- 2
node_per_link <- ceiling(x / u)
est2 <- fitdistrplus::fitdist(node_per_link, "exp")

df <- tibble(lambda_node = round(est2$estimate, 2),
             p_r = round(n_link/sum(node_per_link), 2),
             p_b = round(pexp(u, lambda_pixel), 2))

print(df)

## # A tibble: 1 x 3
##   lambda_node p_r p_b
##   <dbl> <dbl> <dbl>
## 1      0.63 0.63 0.63
```

Horton’s law and statistical similarity

The authors noted in R2.4:

... we are actually did not evaluate statistical similarity across scales.

Although the authors used Horton’s laws as the ground of criticism, this is a “weaker” version of statistical similarity. If two random variables X and Y are statistically similar, then this suffices the following condition:

$$\frac{E(X)}{E(Y)} = C \quad (\text{S.14})$$

where C is the constant (e.g., Horton’s ratio). However, when the ratio of the expected values of the two random variables is constant, it does not *necessarily* suffice the following equation because an expected value is just the first moment of a probability distribution:

$$X \stackrel{d}{=} CY \tag{S.15}$$

Therefore, Horton’s laws are certainly patterns emerging from scale invariance (statistical similarity), but it is not rigorous evidence of scale-invariance, per definition.

Minor points

L. 225-232 Please see my comment on “scale invariance.” Also, the exponent of A is almost zero (equation (1)) - is this statistically supported? p_r is almost constant along A reflecting this value of exponent.

L. 347 the unscaled p_r is dimensional - correct (this is what is presented in the author’s response)? Otherwise, it should not be equal to λ , which is dimensional.

Figure 3: This figure is inappropriate. p_r must be rescaled using equation (1) to compare across scales.

Additional comment - the scaling exponent of watershed area $\beta = 1 - \frac{\log R_L}{\log R_B}$ (p.143 in Rodríguez-Iturbe and Rinaldo (2001)). Therefore, λ' (and hence p_b) is related to this parameter too. In *finite* networks, changing a value of p_b in simulations will change a value of β .

Data and Codes

Data and codes are available here: https://github.com/aterui/public-proj__review

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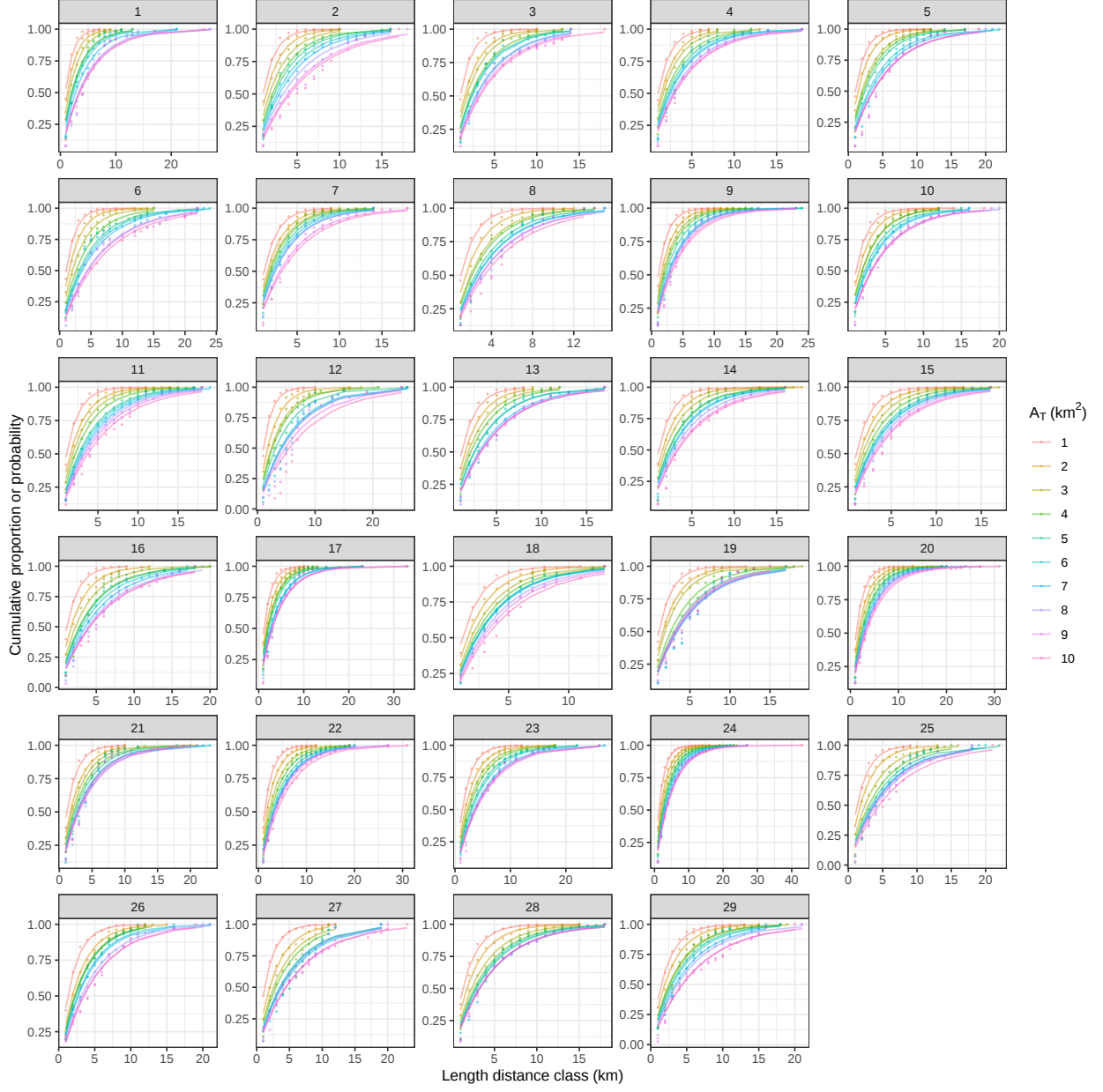


Figure 1: Link length follows an exponential distribution regardless of A_T . Panels indicate 29 example watersheds with watershed area > 500 sq-km (arranged by scaling constant k , and colors indicate different extraction scales A_T). Points are the observed cumulative proportion of a given distance class (distance class 1 km means the proportion of links with < 1 km), and lines are expected values from the fitted exponential distribution ($1 - \exp(-\lambda u)$).

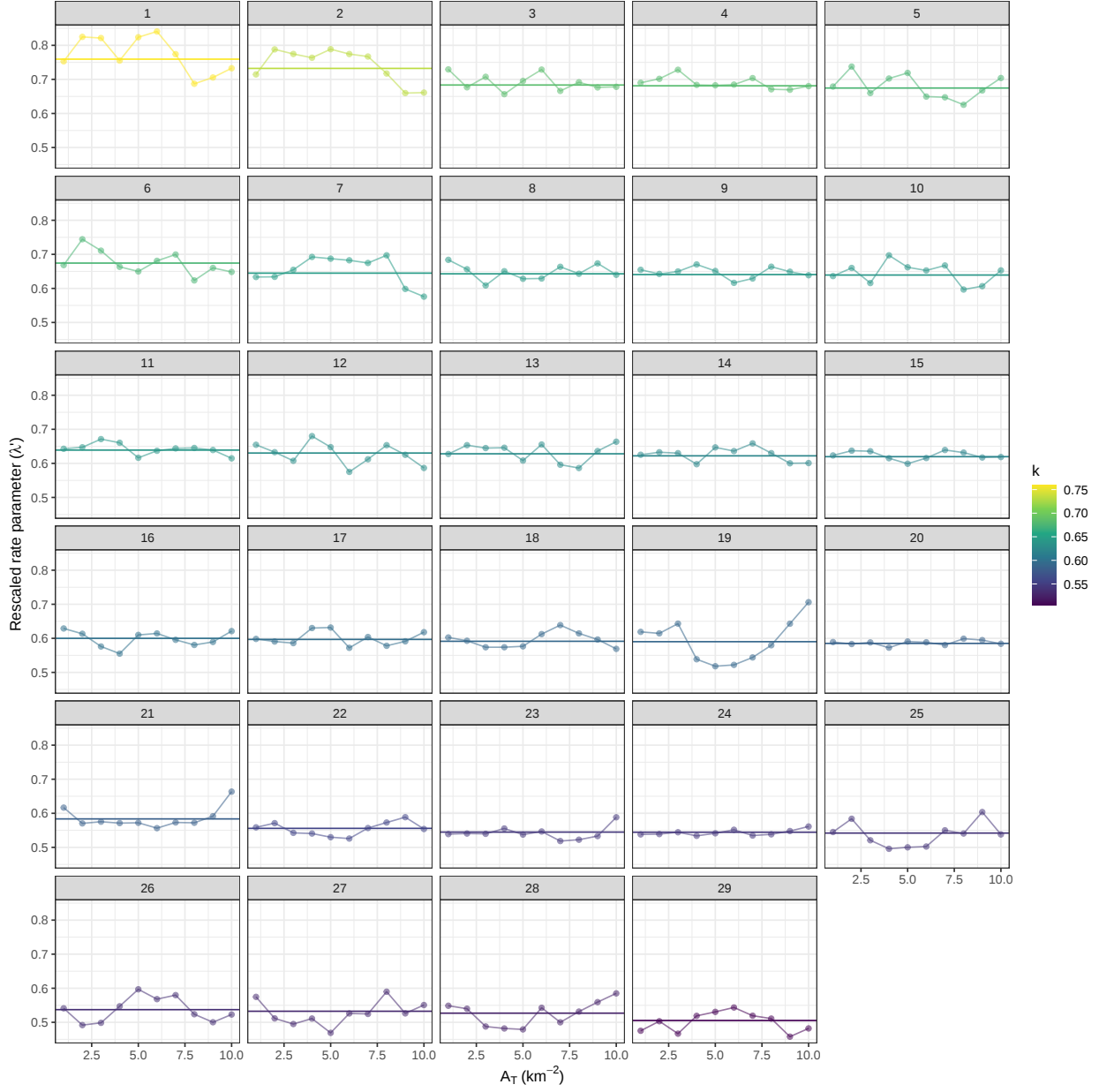


Figure 2: Invariance of rescaled rate parameter λ' . Points are estimates of rescaled rate parameters at A_T . Horizontal lines are the scaling constant k . Panels indicate 29 example watersheds with watershed area > 500 sq-km (arranged by scaling constant k).

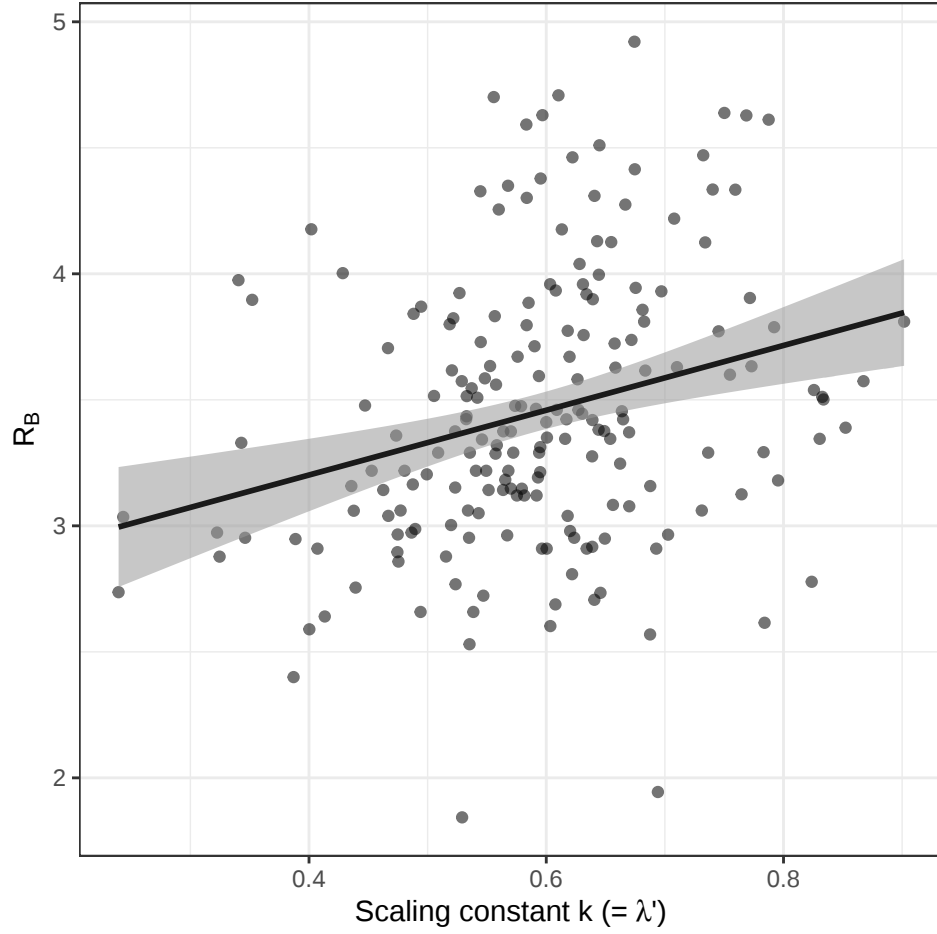


Figure 3: Positive correlation between Horton's branching ratio R_B and scaling constant k ($\approx \lambda'$). Dots represent watersheds. The estimated slope was $\approx 1.29 \pm 0.32$ and was in good agreement with what would be expected from equation S.13.

10th Mar 22

Dear Dr Carraro,

Thank you for your letter concerning your manuscript "The structure of dendritic river networks shapes ecological dynamics", which is being treated as an appeal.

The editor will consider the matter at the earliest opportunity. However please note that, by policy, new submissions must take priority over appeals. Therefore there may be a delay before we respond to you.

Thank you for your patience.

Best regards,

Manuscript Administration
Communications Earth & Environment
4 Crinan Street
London N1 9XW
E-mail: commsenv@nature.com

14th Mar 22

Dear Dr Carraro,

Thank you for your appeal.

You can access your appealed manuscript through the following link:
[link redacted]

Sincerely,

Editor
Communications Earth & Environment
The Macmillan Building
Crinan Street
London N1 9XW

17th Mar 22

Dear Dr Carraro,

We have considered and discussed the points raised in your appeal of our recent decision on your manuscript, titled "The structure of dendritic river networks shapes ecological dynamics". It seems to us that a deadlock has been reached between your arguments and those of Reviewer 1, and we will therefore seek independent advice from an adjudicating referee.

But before we do so, please revise your manuscript in response to the remaining concerns, as appropriate, and supply us with a comprehensive point-by-point response to Reviewer 1's report. We will send your responses, the report and the revised manuscript to the adjudicator.

We would also appreciate suggestions for adjudicators that you have not collaborated with over the past 5 years or so, and who you would trust to be fair. Please supply at least six names — we cannot promise to use any of them, but we will do so if it seems possible and appropriate.

I would be grateful if you could e-mail the revised documents to me at your earliest convenience.

Best regards,

Clare

Dr Clare Davis
Senior Editor
Communications Earth & Environment

Reply to the Reviewer

Reviewer's comments are in black roman type; our replies are in **blue roman type**. For cross-referencing, our replies are labelled as **RX**, where X is the progressive reply number.

Reviewer's comments

General comment. Thank you so much for addressing my concerns. I appreciate the time they have taken for this revision. I have reviewed this manuscript carefully again. First of all, I have to admit that I am not a "true" expert of this research area; I have not been trained formally (I taught myself through readings) nor worked with geomorphologists so far. Hence it is certainly possible that my comments are entirely wrong. If this is the case, please let me know and I'd be happy to communicate with the editor. However, although my knowledge in this field is limited, I believe the following points are worth of further consideration.

According to Rodríguez-Iturbe and Rinaldo 2001, scale invariance is defined as "...The concept of fractals...characterizes those objects in which properly scaled portions are identical...to the original object. In river basins, we will always deal with the statistical description of components and thus the 'fractal' scaling property refers to the invariance of the probability distributions describing the object's composition under geometric transformations or changes of scale." - p. 99 in Rodríguez-Iturbe and Rinaldo (2001). From my reading (my apologies if this is my misunderstanding), it sounded like the authors referred to scale invariance as a geometric scaling factor or scaling exponent per se, such as Horton's R and beta (because they are constant; please see my detailed comment why they are constant across scales). If this is the case, I don't believe this is a common definition of scale invariance - the definition presented above is more common (and correct, I believe) in statistics, mathematics, and geomorphology.

If my argument (detailed in the attachment) is correct, this undermines the major conclusion of this manuscript. I appreciate it if the authors could carefully consider my points.

While we agree with the definition of scale invariance proposed by the Reviewer (see also **R5** and **R14**), we maintain our view that branching probability is an inadequate descriptor of river complexity, as well as of stability and persistence of riverine metapopulations. As we show in our following replies, the conclusions of our manuscript are not affected by the Reviewer's comments.

Attached comments. Thank you for addressing my comments. The authors did a great job in clarifying some parts of the manuscript, and I have a better understanding of the manuscript content. However, I'm afraid that the revised manuscript does not address some of my major concerns (I simply have a different opinion on this topic). I described my concerns below.

Metapopulation simulation. I appreciate that the authors included the variation in habitat size in their simulation, and I agree that OCNs have a better extension capacity (e.g., the inclusion of Euclidean distance). However, my primary concern was how they modeled population synchrony, not habitat size. As I wrote in the previous round of review, the authors made an assumption that population synchrony in the metapopulation CV model decreases with distance (and deterministic!) and implied such synchrony is caused exclusively by dispersal (the model itself does not assume the dispersal is the sole cause, but author's interpretation does; L362-363). This is a very strong assumption, requiring extensive support from the literature. However, this is not the case. First, dispersal is not the sole cause of population synchrony. Moran effects, predators, and many other factors contribute to population synchrony because population synchrony is merely a statistical correlation of two population time series (phenomenological). Therefore, it is inappropriate to describe "... α a parameter expressing the mean dispersal distance." A more accurate description would be "... α is the parameter defining the distance decay of population synchrony..." Second, and more importantly, distance dependence in population synchrony is not well supported in rivers. For example, the population synchrony of salmon within a single watershed shows a vague relationship with river distance. (Braun et al. 2016; Koizumi et al. 2008; Rogers and Schindler 2008). Therefore, expressing population synchrony as a direct function of distance is ecologically unrealistic given the exclusive focus of this study on rivers (distance dependent synchrony may be appropriate in 2D systems though).

R1 Please note that: i) We already discussed about the role of Moran effects and other factors on our results (LL. 271-285). ii) Along-stream distance has been used to describe the spatial covariance of any variable measured in streams, including ecological population counts [Zimmerman and Ver Hoef, 2017], and, more importantly, has been shown to be the main descriptor of synchrony of fish populations in a large study including long-term (> 10 years) time-series from 58 river basins across Europe [Larsen et al., 2021]. We now added a comment in the manuscript where we explicitly mention that our assumption on distance dependence of population covariance is well supported in literature (LL. 365-368). This Reviewer's comment is thus unjustified. See also **R3** with respect to our model's assumptions.

R2 As for the comment on the definition of α , this is a correct suggestion. We have revised the manuscript accordingly (L. 363).

A fair comparison of metapopulation CV with different river metrics (BBT, RBN, and OCN) would therefore need “bottom-up” modeling, where local population dynamics (e.g., Beverton-Holt with density-dependent terms in population growth), environmental stochasticity and similarity, and dispersal (inter-patch movement of individuals) are explicitly modeled. Population synchrony should be treated as the emergent property of these ecological processes.

R3 Please note that a given pattern can emerge from a model only if the related mechanism is taken into account in the model formulation. For example, if dispersal is modelled as a process independent of between-patch distance, no decay of synchrony with increasing distance could emerge from such a model (which would resemble the spatially implicit Levins model). If environmental stochasticity is included, this would not have an impact on synchrony if every patch were affected by a stochastic forcing independent of that of the neighboring patches; if instead environmental stochasticity (as customary in geospatial analyses) is modelled as a process whose spatial covariance decreases with increasing distance, then the metapopulation model could produce patterns of decreasing population synchrony with increasing distance. Our formulation of the coefficient of variation of a metapopulation implicitly assumes that environmental stochasticity affects the fluctuations in the abundance of a local population, which is indeed characterized by a mean μ_i and a variance σ_i^2 . We acknowledge that an arguably more realistic assumption would consider covariances of a stochastic environmental forcing decaying with Euclidean (rather than along-stream) distances; however, comparison between the different network types would be impossible under this assumption, as BBTs and RBNs lack the definition of Euclidean distances.

In my previous simulation, in which I modeled these processes explicitly, the distance dependence in population synchrony did not appear (at least, very vague) in simulated river networks (see SI in (Terui et al. 2018)).

I am not suggesting that the authors must re-perform the analysis (because their focus is not ecological modeling per se). However, the authors should mention how the violation of distance-dependent synchrony would affect the simulation results (which is often true in rivers). Under the author’s metapopulation model, I anticipate there will be a less (and perhaps negligible) difference among BBT, RBN, and OCN with a noisy or no distance dependence in population synchrony. Please note that the distance dependence assumption would be reasonable in the case of metapopulation capacity because it deals with colonization, which may be tightly linked to dispersal (clearly distance-dependent) in most scenarios.

R4 The metapopulation model in Terui et al. [2018] assumed that the correlation coefficient between two patches only depended on whether the two nodes were located in the same branch or not. No spatial effect of distance on decay of synchrony was assumed. Hence, it is not surprising that the distance dependence in population synchrony emerged only vaguely in the model simulations (presumably linked to the distinction between between-branch and among-branch correlation coefficients).

Scale invariance Thank you for addressing my concerns. I appreciate the time the authors have taken for this. However, I feel there is miscommunication - partly because of my unclear wording. To avoid further miscommunication, let me define the following terms in analog of structural and functional connectivity:

Term	Interpretation
Structural complexity	Geomorphological complexity of branching pattern of a river network - this measure purely reflects physical properties of rivers, and the perception of organisms is not relevant for this measure
Functional complexity	Ecological complexity of branching pattern that considers the perception of organisms. Different organisms view the same river network differently.

Also let:

Term	Interpretation
u	Given river distance to measure branching probability. Interpretation includes, but not limited to, an "ecological" ruler defining the scale of a population/community. Dimensional.
l	DEM pixel size (length of a side). Dimensional.
A	Entire watershed area. Dimensional.
A_T	Threshold value of watershed area that initiates river lines. Dimensional.
λ	Rate parameter of an exponential distribution for link length. Dimensional.
L	Length of an individual link (random variable). $L \sim Exp(\lambda)$. Dimensional.
L_{total}	Total river length. Dimensional.
N_L	Number of links.
N_{pixel}	Number of river DEM pixels with length l .
N	Number of nodes with length u . Branching or upstream terminal sections ($< u$) still represent one "section" as a node.
p	Theoretical branching probability in a discretized river network.
p_b	Empirical branching probability for a given river length

Issue of structural complexity – Link length distribution. Before the main point, please allow me to clarify the definition of "scale invariance" - I think the authors understand it (likely than I do), so the following explanation is meant just to clarify the argument. I believe scale invariance refers to . . . *The concept of fractals. . . characterizes those objects in which properly scaled portions are identical. . . to the original object. In river basins, we will always deal with the statistical description of components and thus the 'fractal' scaling property refers to the invariance of the probability distributions describing the object's composition under geometric transformations or changes of scale.* - p. 99 in Rodríguez-Iturbe and Rinaldo (2001).

R5 We of course agree with the definition of scale invariance here reported, and with the following example on power-law distributions (which are the only distributions leading to a scale-invariant behavior [Newman, 2005]). The concept of scale invariance is not limited to the fact that some quantities (R_B , R_L , β) are constant, but this is a necessary condition for scale invariance to occur: for instance, if the slope of the probability distribution of drainage area changed for increasing values of drainage area, the resulting distribution would no longer be scale invariant.

In the following, I refer to scale invariance as the invariance of the probability distributions (or functions) across scales after proper rescaling (see also p.146 in Rodríguez-Iturbe and Rinaldo 2001 for self-affine process, which has different scaling exponents for different axes). In line with this definition, the following function has a feature of scale invariance:

$$f(\psi x) = \psi^z f(x)$$

where ψ is the scaling factor. A power law function would be the most famous example:

$$\begin{aligned} y &\approx f(x) = kx^z \\ y &\approx f(\psi x) = k(\psi x)^z = \psi^z kx^z = \psi^z f(x) \end{aligned}$$

where z is the scaling exponent, k the scaling constant. Now, let me speak about the property of *link length*. The rate parameter for the link length distribution λ follows a power-law of A_T , as shown by the authors (equation (1) in the main text):

$$E(p_r) = \lambda \approx kA_T^z$$

Please note that I ignored the term $A^{-0.032}$ in equation (1) because A is constant when evaluating scale invariance in a given watershed with a fixed pixel size l . Also, $E(p_r) = \lambda$ was shown by the authors - see R.2.3 in their response letter (they wrote $p_r = 1/\lambda$, but I think this is an error... the mean link length is λ^{-1} , so $p_r = N_L/N = N_L/(N_L\lambda^{-1} = \lambda)$. The λ becomes a constant across A_T after proper scaling: $\lambda' = \lambda/A_T^z \approx k$.

R6 This is exactly what we show in our Eq. (1): branching probability scales as a power law of A_T . Note that λ' is dimensional, as it depends on the unit used to express λ and A_T . The nondimensional quantity here is z , which would be analogous to the scaling exponent for drainage areas β . This is the quantity that is preserved across scales, and is independent of the "ruler" used to measure link lengths and areas. The Reviewer is right with respect to the typo in our previous reply; thanks for noticing that.

The part and the whole look alike. I did a poor job in explaining what the "proper rescaling" meant, but what I meant was the rescaling of the rate parameter by A_T or stream order, not changing l subjectively (if we do this, any statistical quantity can be constant across scales... obviously inappropriate). Along this line, if we compare λ at $A_T = a_1$ and a_2 (λ_{a_1} and λ_{a_2} , respectively), the two becomes identical after simple scaling:

$$\lambda_{a_1} = \left(\frac{a_1}{a_2}\right)^z \lambda_{a_2}$$

Peckham and Gupta (1999) proved that, if link length L measured at one specific discrete scale (i.e., stream order ω) follows an exponential distribution, then the link length measured at another discrete scale also

follows an exponential distribution with a different mean (but the mean changes predictably). Given that $z = -\log R_L / \log R_A$ ($R_A = A_T(\omega + 1) / A_T(\omega)$), a similar phenomenon should occur across continuous scales A_T ; indeed, the link length distribution followed an exponential distribution regardless of A_T in Hokkaido, Japan (Figure 1). Therefore, the "rescaled" non-dimensional link length $L' = L / A_T^z$ (random variable) suffices the following equation: $L' \sim \text{Exp}(\lambda')$.

R7 This is simply not correct. It is false that L' is non-dimensional. If L is measured in km and A_T in km^2 , then L is expressed in km^{1-2z} .

Alternative expression would be:

$$L_{a_1} \stackrel{d}{=} \left(\frac{a_2}{a_1} \right)^z L_{a_2} \left(\approx \frac{\lambda_{a_2}}{\lambda_{a_1}} L_{a_2} \right)$$

where $\stackrel{d}{=}$ indicates the equality in probability distribution. In this example, the scaling factor is the ratio of A_T : $\psi = a_2 / a_1$. Therefore, the rate parameter and associated distribution change predictably across scales, and such geometric transformation is defined by the ratio of A_T and the exponent z .

To confirm the above argument, I extracted stream networks of 197 watersheds in Hokkaido, Japan, with 10 values of A_T (MERIT Hydro was used for extraction (Yamazaki et al. 2019)). I estimated the rate parameter at each extraction scale ($A_T = 1, 2, 3, \dots, 10 \text{ km}^2$). Then, the following model was fitted to the data to estimate the scaling exponent and constant for watershed j :

$$\begin{aligned} \ln \lambda_i &\sim \text{Normal}(\mu_i, \sigma^2) \\ \mu &= \ln k_{j(i)} + z_{j(i)} \ln A_{T,i} \end{aligned}$$

In this model, I allowed $\ln k_j$ and z_j to vary by watershed (i.e., random intercept and slope) so that I can estimate watershed specific values. We estimated the rescaled rate parameter $\hat{\lambda}'$ based on the estimated z and the rate parameter λ_1 estimated at $A_T = 1 \text{ km}^2$ ($\hat{\lambda}' = \lambda_1 / A_T^z$). As expected, the estimated $\hat{\lambda}'$ was consistent with k and did not show systematic changes across scales at all the watersheds (Figure 2; fluctuations may be caused by statistical uncertainty). In addition, λ_1 and the scaling constant k were closely associated (Spearman's rank correlation = 0.83, $n = 197$), two parameters that should in theory be identical in the absence of statistical uncertainty (see Equation S.5). The high correlation of these two parameters indicates that the rate parameter estimated at one specific scale can represent the rate parameters measured at other scales (statistically speaking, k is the geometric mean of rescaled rate parameters λ' across scales).

R8 This Reviewer's analysis is indeed interesting, and it confirms that λ scales as a power law of threshold area A_T , which we show in Eq. (1) of our manuscript. However, we are afraid that the criticism raised here is out of scope with respect to our manuscript's content. Our main point is that, while it is clear what one means by referring to "a river with $R_B = 4$ ", or "a river with $\beta = 0.43$ ", since there is no need to specify at which scale these values were evaluated, generating a RBN with branching probability equal to 0.6, or

claiming that a given real river has branching probability equal to 0.5 is an unclear piece of information as long as the scale at which branching probability is assessed is not specified.

The above exercise is essentially the same as what I presented in the previous round of review - in the last comment, I used the Strahler ordering scheme to make the argument simple. The only difference is whether the observation scale is expressed in a discrete (stream order) or continuous form (A_T). If we use the Strahler order (denoted by ω and ξ) instead of A_T , then it becomes (equation 26 in Peckham and Gupta (1999)):

$$L_\omega \stackrel{d}{=} R_L^{\omega-\xi} L_\xi$$

where R_L is Horton's length ratio, which is defined by the average link length (= the inverse of rate parameter λ_1) at two consecutive stream orders:

$$R_L = \frac{\lambda_{\omega+1}^{-1}}{\lambda_\omega^{-1}} = \frac{\lambda_\omega}{\lambda_{\omega+1}}$$

In this sense, I noted in the last review as "... what the authors performed in Fig. 1 is similar to the above exercise - they pruned smaller tributaries from the network by increasing A_T ." Both exercises follow the same principle, and the multiplication of a common factor (either $(a_2/a_1)^z$ or $R_L^{\omega_\xi}$) leads to the invariance of the link length distribution across scales. As I noted above, z is a function of R_L ($z = -\log R_L / \log R_A$).

The authors claimed that λ (and hence, branching probability) changes with A_T , and this is the main reason why this metric is not an inherent property; however, I am not saying that each river network has a unique λ without rescaling (and no measurable, dimensional quantity satisfies this condition... I believe...). What I am saying is that the rate parameter λ (and therefore the distribution of link length) is a statistical quantity derived from a fractal scaling property of river basins.

R9 We definitely agree with this: λ depends on the scale at which link lengths are measured; the rescaled (dimensional) λ' is a dimensional quantity that does not depend on A_T by construction; the nondimensional quantity that is preserved across scales is the exponent z (see **R6**). As a consequence, neither λ nor λ' can be considered as metrics driving the stability of a riverine metapopulation: indeed, λ depends on the observational scale, while λ' for a given river oscillates stochastically for different A_T values around an average value independent of A_T ; as we note in **R17**, comparing different rivers in terms of "rescaled" branching probability would lead to different rivers ranking differently as A_T changes.

While λ' is independent of R_L , it is important to note that R_B is a function of λ' and R_L , at least in random topology models. Peckham (1995) (see equation 6) has derived the following equation based on Tokunaga's model

$$R_B = \frac{(2 + \lambda' + R_L) + \sqrt{(2 + \lambda' + R_L)^2 - 8R_L}}{2}$$

It is clear from this equation that R_B is an increasing function of λ' (in equation 6 in their paper, notice that $a = \lambda'$ and $c = R_L$). Indeed, R_B was positively associated with λ' in Hokkaido (Figure 3).

From my reading (my apologies if this is my misunderstanding), it sounded like the authors referred to scale invariance as a geometric scaling factor or scaling exponent per se, such as R_L and z . If this is the case, I don't believe this is a common definition of scale invariance - the definition presented above is more common (and correct, I believe) in statistics, mathematics, and geomorphology. The constant values of R_L and z emerge as a result of statistical self-similarity (see Horton's law and statistical similarity). They are already "properly scaled" quantities by taking a ratio of dimensional quantities of consecutive stream orders (in response to the author's claim in R2.4).

R10 We respectfully disagree with the formula presented by the Reviewer. In the paper by Peckham mentioned by the Reviewer, a and c are the parameters of the relationships $T_k = ac^{k-1}$, where T_k is the number of side tributaries of order $\omega - k$ entering a link of order ω . This has absolutely nothing to do with the length ratio and the branching probability. Please see also our replies **R5** and **R14** with respect to the generalized definition of scale invariance.

Branching probability. Let me define branching probability as $p_b = 1 - \exp(-\lambda u)$ for now (see section *Branching ratio* for more discussion). Assuming the above argument is correct, the rescaled, non-dimensional rate parameter characterizes the structural complexity of a river network across scales. The rescaled branching probability $p'_b = 1 - \exp(-\lambda' u')$ is therefore non-dimensional and constant across scales (at least, in theory). Note that the length scale used to measure branching probability (u') becomes non-dimensional because it is measured in the unit of λ' .

As far as we are concerned about structural complexity, there is no need to define the scale of population/community, and the rescaled branching probability simply means the probability of $L' < u'$. For this reason, I still think branching probability is a reasonable measure to approximate environmental heterogeneity or any other factors related to branching patterns.

R11 Again, we respectfully disagree. As stated in **R6**, λ' is a dimensional quantity, and so is u' . Moreover, and more importantly, if defined as $p'_b = 1 - \exp(-\lambda' u')$, branching probability depends on an arbitrary quantity u' , which should not be the case if one wants to use this quantity as a metric to assess river complexity.

Issue of ecological complexity. Yet, the use of branching probability would be complicated when it comes to "ecological complexity." We need to define an ecologically relevant "characteristic scale," and different species may recognize the same (rescaled) branching probability differently. However, I don't believe this is a problem unique to branching probability because R_B is a function of λ' . For example, species that prefer smaller tributaries may benefit from higher R_B , but species that prefer larger streams

may not, as noted by the authors (L.154-161). Therefore, different species will recognize the same value of R_B (and R_L) differently. Also, recall that R_B and R_L defines the scaling exponent of watershed area ($\beta = 1 - \log R_L / \log R_B$) and fractal dimension D ($D = \log R_B / \log R_L$) (p.143 in Rodriguez-Iturbe and Rinaldo (2001)). Thus this argument is pertinent to all the other metrics.

I understand the author's claim that organism's perception is dimensional, and I totally agree with this point. However, if this is a problem to branching probability, then it is a problem for other measures of fractal scaling properties too. Once we consider the influence of fractal properties on species, the organism's perception plays a role, and the resultant outcome is no longer non-dimensional (because we have to think about fractal measures relative to the organism's perception). Therefore, the point raised by the authors is not a problem unique to branching probability. It is a problem with all the fractal scaling properties of rivers.

R12 It is not correct that R_B depends on λ' (see **R10**). While we agree that different species could have different perceptions of the same river network (as we already comment in LL. 138-147), we do not see how this would change the "perceived" values of the topological and scaling metrics of rivers. For instance, if a fish does not enter reaches with stream order equal to 1, then its "perceived" will have the same R_B value of the original river network, because $N_1/N_2 = N_3/N_2 = R_B$ by definition.

Branching ratio. Thank you for the detailed explanation. I was implicitly assuming $u > l$ in my comment, and it has caused confusion. My apologies. The following is not a comment requesting a revision, but let me clarify the miscommunication regarding the relationship between p_r and $p_b (= 1 - \exp(-\lambda u))$. My understanding is that the authors intended to provide a proxy of branching probability that is measurable in real river networks so that theoretical branching probability $p \approx p_r$. Mine too.

To give an example, let me assume the DEM with pixel size l is acceptably accurate [$l = 0.03$ km, for example], such that the "true" total river length equals the number of river DEM pixels ($L_{total}[pixel] \approx N_{pixel}$). Also, I assume a single value of A_T , as it does not change the following argument. Assuming $u > l$ (e.g., $u = 100[pixel]$), defining branching probability as $p_r = N_L/N$ means that river sections shorter than u represent branching nodes (therefore, $uN > N_{pixel}$). The same quantity can be measured differently. Using the accurate river network, we can estimate the average link length λ_{pixel}^{-1} [pixel] by assuming the link length $L[pixel]$ follows an exponential distribution. Then, $p_r = N_L/N = 1 - \exp(-\lambda_{pixel}u) = p_b$ or $\lambda_{pixel} = -\ln(1 - p_b)$ because both metrics assume that a river section with $< u$ represents one branching node. I agree with the ecological problem of this definition.

In the meantime, in R2.3, the authors state "... the left side of Eq. (1) is not the branching probability..." and wrote $p_r = N_L/(N_L\lambda^{-1}) = \lambda$. This equation holds true only when $u = l$ because it assumes $N_L\lambda^{-1} = N_{pixel} = N$ in the denominator. As $l \rightarrow u$, the number of nodes within each link (= link length $L[node]$) will decrease such that $\lambda_{node}[node] = p_r = 1 - \exp(-\lambda_{pixel}u)$, where $L[node] \sim \exp(\lambda_{node})$. So,

what I suggested is identical to author's metric when $u > l$. When I extract river networks, I often use resolutions that are fine enough to capture headwater tributaries (e.g., 30m or 90m) - so $u > l$ was always the case. I think our metrics are compatible - just a different assumption.

Example:

```
# "true" link length distribution
lambda <- 0.5
n_link <- 1000
x <- rexp(n_link, rate = lambda)
# fitting exponential to true link length
est1 <- fitdistrplus::fitdist(x, "exp")
lambda_pixel <- est1$estimate
# discretize by u; assuming u >> 1
# fitting exponential to link length measured in number of nodes with length u
u <- 2
node_per_link <- ceiling(x / u)
est2 <- fitdistrplus::fitdist(node_per_link, "exp")
df <- tibble(lambda_node = round(est2$estimate, 2),
p_r = round(n_link/sum(node_per_link), 2),
p_b = round(pexp(u, lambda_pixel), 2))
print(df)

## # A tibble: 1 x 3
## lambda_node p_r p_b
## <dbl> <dbl> <dbl>
## 1 0.63 0.63 0.63
```

R13 We note that the approach proposed by the Reviewer induces a deformation to link lengths, in particular when the number of nodes per link is calculated as `node_per_link <- ceiling(x / u)`: all links that are shorter than u are elongated to a length equal to u . We already commented and resolved this aspect in our first round of replies (see R13 and R14 therein).

Horton's law and statistical similarity. The authors noted in R2.4: "...we are actually did not evaluate statistical similarity across scales." Although the authors used Horton's laws as the ground of criticism, this is a "weaker" version of statistical similarity. If two random variables X and Y are statistically similar, then this suffices the following condition:

$$\frac{E(X)}{E(Y)} = C$$

where C is the constant (e.g., Horton's ratio). However, when the ratio of the expected values of the two random variables is constant, it does not necessarily suffice the following equation because an expected value is just the first moment of a probability distribution:

$$X \stackrel{d}{=} CY$$

Therefore, Horton's laws are certainly patterns emerging from scale invariance (statistical similarity), but it is not rigorous evidence of scale-invariance, per definition.

R14 As we already stated in the previous round of replies, we agree with the "generalized" definition of self-statistical similarity proposed by Peckham and Gupta [1999], which we are not questioning here. In our manuscript, we more simply aim to show that branching probability is a non-descriptive property of river networks, and it requires the definition of a scale (see the example in **R8**).

Minor points. L. 225-232 Please see my comment on "scale invariance." Also, the exponent of A is almost zero (equation (1)) - is this statistically supported? p_r is almost constant along A reflecting this value of exponent.

R15 The exponent of A was significantly different than 0 based on the fit on four large OCNs (from which Eq. (1) was derived, see Carraro et al. [2020]). As we state in the manuscript, our goal was not to provide a universal relationship valid for any OCN and real river network, but rather showing an example of how branching probability is related to threshold area.

L. 347 the unscaled p_r is dimensional - correct (this is what is presented in the author's response)? Otherwise, it should not be equal to λ , which is dimensional.

R16 $p_r = N_L/N$ is here nondimensional because N is measured in number of pixels, hence implying that a fixed pixel size l is assumed. The same applies to A and A_T when defined in number of pixels.

Figure 3: This figure is inappropriate. p_r must be rescaled using equation (1) to compare across scales.

R17 This is not correct. Actually, the rescaled quantity $\lambda' = \lambda/A_T^z$ was never used to define branching probability in previous studies. For example, in Terui et al. [2018], Fig. 2, one could consider the different branching probability values shown there either as representative of different networks, or of different scales for the same network. In the former case, this would implicitly mean that there exist river networks that are more branching than others—an argument that we confute with our Fig. 3; in the latter case, this would mean that branching probabilities are compared without rescaling them. Importantly, note that, even if we were to divide our p_r values by A_T^z , this would not affect the ranking of rivers in terms of branching probability within a given A_T group (because the A_T values are constant within each group by construction).

Additional comment - the scaling exponent of watershed area $\beta = 1 - \log R_L / \log R_B$ (p.143 in Rodríguez-Iturbe and Rinaldo (2001)). Therefore, λ' (and hence p_b) is related to this parameter too. In finite networks, changing a value of p_b in simulations will change a value of β .

R18 Again, it is not true that R_B is a function of λ' (see **R10**). However, we agree that the exponent z of the relationship $\lambda \sim A_T^z$ should be related to the other known exponents characterizing the power-law scaling of river networks (see e.g. Maritan et al. [1996]). However, this aspect is not really pertinent with respect to our work, which does not discuss value and implications of such exponent.

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19th Apr 22

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REVIEWERS' COMMENTS:

Reviewer #3 (Remarks to the Author):

This manuscript written by Carraro & Altermatt have made a systematic comparative analysis on which kind of the already known methods (including BBT, RBN and OCN) can best capture the topological and scaling features and thus hydrological and ecological dynamics in real riverine networks. They found that only OCNs can yield relevant estimates comparable to real riverine complexity, which I think is interesting and novel for freshwater biologists. Currently, different approaches have been developed to generate riverine networks, but which one can best capture topological complexity of real riverine networks is still unknown. This study provides a systematic comparative analysis on these approaches, which will definitely influence our thinking in both conceptual understanding and technological capability.

After reading the revised manuscript as well as the rebuttal letter, I think the method sounds solid and their relevant analysis is convincing, though there are some controversies over the details in Methods from one of previous reviewers. In fact, these controversies don't affect the obtained general conclusions, which I think the previous reviewer also agreed with. This manuscript has already gone through one round of revision, and most of questions raised by reviewers have already been addressed properly by the authors, thus I do not have any question in this manuscript.

I have one suggestion: the title of this manuscript should be changed to match the aim of this ms, e.g., Optimal Channel Networks capture ecological dynamics in real riverine networks.

Overall, I would recommend it for publication in Communications Earth & Environment.

Response to the referee

We are very grateful to the adjudicating reviewer for their supportive assessment of our work. Based on their suggestion, we modified the manuscript title, which now reads “Optimal Channel Networks capture ecological dynamics in dendritic river networks”.